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Ecological Responses to Climate Change at Biogeographical Boundaries

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Abstract

Temporal and spatial biogeographical boundaries are usually associated with extinction processes. However, some boundary regions seem to be places of speciation. It is unclear if boundaries are favored by generalized or specialized species. Recent studies suggest that narrow-ranging species can be strong competitors and they can replace wide-ranging species while shifting their range boundaries under the effect of climate change. In other boundary regions, the decline of both passive- and active-dispersing specialists has been observed. Core regions are also weakening. They are jeopardized mainly by extreme climate events and fragmentation and by the accompanied non-native invasions. Biodiversity loss and homogenization have been observed globally.

Keywords: biogeographical boundary, ecotone, core region, climate change, mass extinction, specialist, generalist

1. Introduction

Temporal and spatial biogeographical patterns change in space and time. Historical biogeographical boundaries usually mark great mass extinction events. The role of spatial boundaries is controversial in recent global changes. Some suggest that species at sharp biogeographical boundaries are at the edge of their existence and doomed to extinction, others allege that transition zones can serve as biodiversity hot spots. They harbor either wide-ranging species adapted to broad environmental circumstances or narrow-ranging species occurring in unique environments. Researchers assuming specialized species in boundary regions imply that biogeographical boundaries are suitable for climate change detection and specialists can be used as early warning signals. Several studies suggest that specialization is the greatest extinction risk [1]. However, mass extinction events affect both specialized

and generalized species. Studies show that both groups are declining under global changes. Interactions between specialists and generalists are not exactly clear. It is urgent to detect their locations globally and clarify their roles. It is also an alarming trend that not only boundaries but also core regions are weakening, which leads to homogenization, the abundance of generalized species, and biodiversity loss. Recent anthropogenic changes are complex including not only climatic changes but also habitat destruction, fragmentation, and pollution which act synergistically.

This chapter addresses the following issues: (1) Are biogeographical boundaries the scenes of extinction? (2) Which factors weaken spatial boundaries and core regions? (3) Are core areas threatened by climate change? (4) Are biogeographical boundaries unique regions? (5) Do they harbor generalized or specialized species? (6) What are the roles of specialists and generalists in extinction processes?

2. Temporal biogeographical pattern

Temporal and biogeographical boundaries cannot be separated from each other. Temporal boundaries eliminate old spatial boundaries and create new ones. Temporal boundaries are usually associated with extinction processes. It is suggested that mass extinctions start at local scales and spill over to higher scales in time [2].

2.1. Succession

Local species and communities replace each other in time. At ecological time scale, this process is induced by repeated disturbances, and it is called succession. The Clementsian school considers succession as a deterministic process that culminates in a predictable stable, “climax” community [3]. Succession is not random, because it is determined by climatic and soil conditions. In contrast, the stochastic Gleasonian school suggests that a single region can have several successional stages at the same time and more than one stable stages or climaxes [1].

2.2. Mass extinction

Major extinction events indicate boundaries in geological time. Approaching an extinction event, ecosystems display specific traits serving as warning signals of a catastrophic shift. (Post-extinction periods also show distinctive pattern of biotic restructuring.) Extinction events as temporal boundaries eliminate old spatial boundaries and create new ones. Non-catastrophic extinctions affect biological systems at different spatial scales and different trophic levels in a selective way. The inherent extinction proneness of taxa also contributes to the selective nature of extinctions. In contrast, catastrophic extinction events or, in other words, mass extinctions affect the whole global ecosystem in a non-selective way wiping out most living creatures. Several studies suggest that we are undergoing the sixth mass extinction.

Non-selectivity is the main characteristic that makes a difference between background and mass extinction. During mass extinction events, widespread and abundant species also extinct

[4, 5]. The disappearance of generalists is a sign of shifting toward nonselectivity [6, 7]. (Large body as a main extinction trait is often mentioned in literature; therefore, losing large-body mammals [8] is an early indicator.)

At global spatial scale and at longer time period (historical time scale), sudden and large environmental perturbations wipe out whole biotas causing mass extinction. This large-scale, repeated replacement is similar to local succession. Apart from mass extinctions, changes in biotas are of smaller magnitude and rather gradual. That is why an increase in frequency and magnitude of changes in communities or biotas is an early signal of a regime shift. At geological time scale, mass extinctions usually mark a boundary between time units (e.g., eras, period, epochs), the tipping point of a biotic shift. They are associated with drastic environmental perturbations (sudden climate change, volcanism, sea-level changes, meteor impact events). Referring back to recent climatic changes, historical mass extinctions accompanied with global warming can provide valuable information for us to be able to presage future trends.

3. Spatial biogeographical pattern

The geographic ranges of species evolve under limited environmental conditions creating a spatial pattern. Broad-ranging species perceive fewer boundaries than species with restricted geographic ranges, and they can shift their ranges relatively more easily under changing environmental conditions.

Spatial boundaries are affected by natural biotic and abiotic factors and anthropogenic disturbance which enhance each other's effect through interactions. Extreme changes in these factors and in the inherent traits of boundaries can lead to extinctions.

3.1. Abiotic factors

The abundance and the distribution of species are usually affected by the synergy of multiple environmental factors, such as temperature, water availability, soil and water chemistry, etc. For example, the tolerance of high temperature is typically lower in plants, which don't tolerate decreased soil moisture. Local extinctions at the boundaries of species ranges are common during droughts [1, 9, 10].

3.1.1. *Extreme perturbation*

Disturbances such as fires, storms, and volcanic eruptions either destroy or maintain boundaries, depending on their magnitude and frequency. Natural ignition (lightning), for example, prevents woody encroachment and exotic species invasion at forest and shrub/grassland boundaries; therefore, artificial fire suppression leads to forest expansion. In arid regions, the decrease in natural *fires* coupled with livestock grazing often results in desertification. Desert shrublands expand at the expense of grasslands [1, 11, 12]. Synergistic processes have an important role in this case as well. Fragmentation lowers the probability of lightning-ignited

fires. Increased fragmentation along with the disappearance of an important boundary regulator leads to the local extinctions of native grassland species which can spill over to higher spatial levels supporting the homogenization processes.

The investigations conducted by du Toit et al. [13] in the South African Nama Karoo transition zone confirmed that more frequent and/or more intensive fires can lead to a biome shift if the most abundant species fails to recover after an extreme disturbance in a transition zone. The dominant vegetation of Nama Karoo is grass, and shrub and fires are rare. They monitored the recovery of the vegetation after a natural ignition. Most of the species managed to recover except the most abundant Karoo shrub species seven months after the fire. This might suggest a biome shift from shrubland to grassland.

3.1.2. *Extreme weather pattern*

Climate change enhances the magnitude and the frequency of extreme events [14]. Frequent extreme climatic events, e.g., extreme droughts, weaken both core areas and boundary regions by altering species composition, diversity, and functional and structural attributes. Native species being less adaptive to extreme events may be displaced by non-native generalist invaders [15].

Boundaries are more exposed to extreme events than core regions; therefore, even the events of low magnitude can degrade their structure. Several studies confirm that relatively weak winds can contribute to the invasion of weedy species by dropping wind-transported seeds at the edges [16, 17].

Recent *droughts* have induced forest canopy thinning in the core areas of tropical forests. In some high-rainfall places, forests have disappeared probably because of the relatively long dry season in Australia [18, 19]. Longer dry periods have also been experienced in tropical montane forests in Costa Rica with severe consequences [20]. Drier climatic conditions opened a path for pathogenic invaders from lower altitudes [21] resulted in the die-off of most endemic frog and toad species during the 1980s [22]. This example illustrates the devastating effects of synergistic extinction drivers on endemic species. According to Fjeldså [23], the lack of endemic species in a tropical montane forest indicates that the local biotic community cannot maintain a hydrological balance anymore and withstand global changes.

3.1.3. *Habitat destruction and fragmentation*

Habitat destruction and fragmentation can be considered as extreme anthropogenic perturbation. Fragmentation is detrimental for specialized species. It eliminates intact core zones and reduces the imperviousness of edges providing open space for non-native, wide-ranging species. The higher trophic level and large body size make terrestrial species sensitive to fragmentation. This can further enhance the extinction proneness of African megaherbivores maintaining biome boundaries.

Janzen [24] confirmed that fragmentation leads to *weed expansion* in habitat patches. Forest fragmentation results in smaller patches which probably become more and more distinct

from the intact forest, because the mortality of native tree species along the edges is higher than that of environmentally more tolerant weedy species [24]. The success of weed invasion depends on the width and the imperviousness of buffer zones as well as their relative dispersal abilities [25]. Buffer zones are the zones between the core areas and edges, or, in another point of view, they can be considered as wider edge zones. If they are occupied by weedy species, native interior tree species cannot reestablish [26]. In small patches, forest specialists can be completely replaced by generalists after perturbation [27]. Conservationists emphasize that it is important to preserve larger habitat patches which presumably contain more specialist species. Nevertheless, Beier et al. [28] pointed out that the generalists inhabiting small habitat patches provide important ecosystem services; therefore, they can be the centers for future ecosystem recovery [28].

In general, higher trophic levels give stronger responses to fragmentation and habitat loss than lower trophic levels [29–31]. Krauss et al. [32] assume that lower population sizes, higher population variability, and dependence on lower trophic levels are the main reasons for fragmentation susceptibility of higher trophic levels. Large body size can also enhance the sensitivity to fragmentation and increase the extinction risk of terrestrial species according to several sources [33].

3.2. Biotic factors

The main biotic factors forming boundaries are *competition, predation, and mutualism*.

3.2.1. Competition

Species limit each other's distribution by *competition*. Strong competition can result in non-overlapping range boundaries [1]. Non-overlapping boundaries display sudden regime shifts under environmental changes. The current shifting of species ranges is also influenced by competition, which affects both the generalized and specialized species.

In the last decades, woody encroachment has been experienced globally under the effects of global warming [34–36] mainly because of CO₂ enrichment. Woody species which are generally superior competitors [1, 37] tend to be sensitive to abiotic stress (fire, drought). However, they experienced fewer detrimental perturbations recently, which also helped their expansion.

The relationship between species diversity and geographic range limitation affects spatial patterns [1]. Abiotic and biotic factors vary along range boundaries. Under unfavorable environmental conditions, species diversity and hence competition are lower. When environmental conditions are beneficial for most species, diversity increases and biotic interactions (e.g., competition, predation) will become the limiting factors. This might be the reason why many biodiversity hot spots are located along the tropical biome boundaries.

The global spatial pattern of generalist and specialist species reflects the changing abiotic conditions in a similar way. In the tropical zone where the environmental conditions are favorable, the diversity and the biotic interactions are high, many species tend to be specialized, and the ecosystems are productive. Proceeding to the poles, environmental conditions

become more unfavorable, diversity and productivity decrease, and the species become more generalized. Isolated and small geographic ranges (small islands and forest fragments) are also homogenized and dominated by a few generalized species because of the unfavorable conditions. Decreasing geographic ranges and increasing disturbance jeopardize both specialized and generalized species.

The tropical region provides interesting examples for diffuse competition which also modifies species ranges under recent climate change. Proceeding to the equator, the southern limits of the geographical ranges become less climate dependent and more effective by competition in the Northern Hemisphere. MacArthur et al. [38] suggest that strong biotic competition restricts some tropical species to habitats with less favorable environmental conditions. The same species can turn into widespread and abundant species in subtropical and temperate zones by diffuse competition. Yellow warbler (*Dendroica petechia*) is a good example for that. Its geographic range is widely expanded in the temperate zone, while under tropic conditions, it is strongly restricted [38]. According to MacArthur et al. [38], diffuse competition of tropical species is on increase.

Bennett et al. [37] also observed strong tropical competitors in the temperate zone. Tropical herbivorous fish shifted northward at the expense of seaweeds. Seaweeds are dominant, wide-spreading taxa in subtropical and temperate coastal zones. The poleward shift of tropical herbivorous fish prevents the recovery of seaweeds and maintains a canopy-free alternative state after the extreme disturbances (overgrazing).

In some cold regions, specialists are displacing generalized species. Directional taxonomic shifts of the algal communities in the Northern Hemisphere have been observed by Ruhland et al. [39], especially in the alpine regions and arctic zones with a tendency of an increase in specialized taxa which are replacing generalized species [40].

3.2.2. Predation

Predation can limit the distribution of both predators and preys. Specialization or overhunting can lead to a drop in prey abundance, and this way both groups suffer. The geographical ranges of highly specialized predators are usually further constricted by other limiting factors; hence, they are especially prone to extinction.

3.2.3. Mutualism

Mutualism results in the identical ranges of parasites and hosts; therefore, coevolved species at boundaries and in core regions are prone to co-extinction. Mutualism-related co-extinction is strongly enhanced by fragmentation. Co-extinction affects both specialist and generalists, which can lead to wider extinction.

Grasslands are endangered globally. Grassland specialists can expect a long-term decline because of the drastic loss of their habitats [32]. Time-delayed extinction of long-lived vascular plants may bring about the co-extinction of short-lived specialized herbivores, e.g., butterflies [32].

Rainforests are also jeopardized by habitat destruction. The decline of old native trees in rainforests because of fragmentation may cause the co-extinction of specialized mutualists and herbivores [41].

Invasion can replace core super-generalists in the mutual networks, as well. Giannini et al. [42] observed invasive super-generalist bee species in Brazil replacing native super-generalist species which can modify the interactions in networks. The non-native, super-generalist bee species invaded into the core of the networks rapidly. Romanuk et al. [43] and Lurgi et al. [44] suggest that large and more generalist species are the best invaders.

Dario Palacio et al. [45] studied a highly diverse network of plant and fruit-eating birds in a cloud forest in the Colombian Andes. They found that the elimination of super-generalists which are the connectors of disconnected subsets of species makes the mutualistic network prone to collapse despite its high diversity. They experienced the early decline of large frugivores forming the core of the network because of their high vulnerability to fragmentation. They also noted that the early loss of endemic and specialized species may precede the decline of central super-generalists. However, the extinction of less-connected specialized species presumably does not lead to the collapse of the whole network in contrast with the decline of the central super-generalist species. Similar networks are located in the Atlantic Forest in Brazil as well which are also threatened by extinction [46]. The authors' results suggest that generalist species play an important role in the ecosystem functions.

3.2.4. *Dispersal abilities*

Both active- and passive-dispersing specialist species are declining. Specialist species are at great risk even if they are active dispersal.

Good dispersals are able to shift their ranges and avoid abiotic stress. For this reason, the natural range boundaries of plants and sessile animals change relatively slowly. For instance, the contemporary biome distribution pattern in Africa does not reflect the actual current climate but historical conditions [47].

According to Terborgh [48], mainly specialization, high trophic level, and poor dispersal ability promote extinction. Laurance [49] and Turner et al. [50] suggest that mammals and plants with poor dispersing abilities are more prone to extinction than active dispersers, which leads to a higher abundance of generalist species [51]. Wilson and Willis [51] highlight the early loss of specialists during extinction events. Short-lived pollinators with good dispersal abilities shifted their ranges in North America and Europe under climate change [52]. Short-lived specialists are sensitive to environmental changes [53], which makes them good early warning indicators of perturbation. Bartomeus et al. [54] described a decline in plant-pollinator networks throughout the US over the last 120 years. Scheffers et al. [55] suggest that specialized pollination systems are expected to be more vulnerable and hence more sensitive indicators of global warming. Krauss et al. [32] found that short-lived specialist butterflies experienced severe decline after perturbation despite the fact that they are active dispersers.

Rare species are usually more localized, sparse, and relatively more specialized [33]. Their geographic ranges are more fragmented; hence, metapopulation and edge effects can be significant contributors of their decline [56]. Specialized taxa tend to be rare, which increases the extinction likelihood [33]. Rarity and specialization are two different traits, but they often act synergistically. However, Didham et al. [57] pointed out that range-restricted species may be more disperse and persistent than common, sessile species in small fragments. Didham et al. [57] investigated the effects of forest fragmentation on beetle species in central Amazonia. They found that rare species were better survivor in small fragments than “common” species. They concluded that rare species are more mobile and more persistent in contrast with competitively dominant but more sessile species which are more prone to extinction under forest fragmentation. Hanski and Ovaskainen [58] argue that the transient abundance of rare species can be experienced after excessive habitat loss and fragmentation.

3.2.5. Sensitive development stages of species

Species at different development stages show different tolerance of environmental conditions, which affects their range sizes, their boundary types, and boundary perception. For example, the life cycle of a frog or a dragonfly includes very different ranges and boundaries because of the varied niches of stages.

Higgins et al. [59] emphasize that the growth rate of Savanna tree seedling and saplings affects their survival during fire events. Fire suppression, especially during the sensitive development stages of trees, favors woody encroachment.

3.2.6. Continental drift

The theory of continental drift was formed during the last century. It was a revolutionary step, and it revealed the secret of several vague biogeographical issues, for example, the omnipresence of sessile animals, which are not able to cross oceans. Plate tectonics is responsible for the birth and the destruction of continents. The assemblage and the positions of continents are changing. Their union creates bridges between terrestrial biotas providing free gene flow, and their separation may lead to their isolation. These processes are selective as species are sensitive to boundaries to different degrees especially considering their dispersal abilities, but it can be stated that global changes of large magnitude affect most species uniformly in many cases.

According to Lyell’s geoclimatic theory, the concentration of continents near the equator triggers global warming, while the juxtaposition of landmasses close to the poles evokes global cooling. Hence, continental drift can be considered as a climate regulator and thus a temporal boundary “creator.”

The collision of continental plates can establish a connection between biotas, but paradoxically it can create a spatial boundary as well, since continental collisions produce towering mountain ranges which are restrictive to lowland species. The union of landmasses is a violent event erasing and reshaping boundaries. The Great Permian Extinction may have also been associated with the formation of the Pangea supercontinent which brought about a significant drop in the sea level and the drying of the continental shelves [1]. However, Pangea

also served as a cradle for many survivors and novel species which expanded their range boundaries over the continent. When the continents separated, global climatic conditions changed dramatically again. The species survived this event radiated and diversified under new environmental circumstances.

4. Some important spatial traits of biogeographical boundaries

Biogeographical boundaries can be categorized in many ways [60, 61]. Here, mainly sharp boundaries are discussed in relation to global changes.

Controversial views on boundaries are partly generated by incoherent spatial scales applied in studies.

4.1. Spatial scale

Climate has a great effect on the biogeographical pattern. Geography and meteorology apply similar spatial scales which makes the scientific investigations more consistent. Saunders and Briggs [62] emphasize the importance of proper scale. If biogeographical problems are not managed at the proper scale, it can lead to the loss of biota. The mismatches of human-related and natural boundaries can deteriorate the environment. Improper scale also brings about biased and controversial data.

Sub-local spatial scale (< a few meters) includes microhabitats and small boundaries. For example, the boundaries between surfaces of different exposures on a boulder also mark the borders between the patches of different lichens. Local spatial scale (a few meters to 1 km) deals with the level of communities. Regional spatial scale (1–100 km) can be related to landscape boundaries, and continental spatial scale (>100 km) is appropriate for researches on landmass boundaries. Increasing spatial scale is usually associated with increasing temporal scale, from a couple of hours or days to millions of years.

4.2. Spatial origin: natural vs. anthropogenic

Natural boundaries are the formations of the nature which divide two or more different units of natural origin, like timberlines, mountain chains, and watercourses. Anthropogenic boundaries are usually man-made objects (transportation, industrial, residential elements) and the boundaries of anthropogenic plant communities (croplands and plantations). Anthropogenic boundaries are always sharp representing an obstacle or filter to migration and gene flow. They can be either physical objects or boundaries of high contrast between the adjacent units, for instance, edges between forests and croplands where different microclimatic and ecological conditions meet.

4.3. Spatial structure: sharp vs. gradual

Nature can produce relatively quick changes at boundaries as well; however, along environmental gradients, abiotic and biotic changes are gradual. This leads to an important difference between

sharp and gradual biogeographical boundaries. They are usually referred to as “ecotones” and “ecoclines” in ecology.

Starting with the latter one, ecoclines are ecosystems in which the associated communities show a gradual change along an environmental gradient. The environmental heterogeneity results in gradual phenotypic and/or genetic differences of species which are also called ecotypes. This gradual variation reflects an adaption to the changing environment. In an ecocline the physiological characteristics of plants and animals change gradually proceeding to higher latitudes (e.g., the skin color in human populations). This phenomenon can lead to speciation only if the environmental conditions change dramatically.

Researchers usually show more interest in ecotones which represent sharp biogeographical boundaries between ecosystems.

5. Ecotones

Sharp boundaries are usually referred to as ecotones in literature. It is suggested that sharp boundaries (hereinafter ecotones) might be unique environments.

Ecotones have been studied for more than a century [63–65]; however, researchers have devoted more attention to the investigation of distinct, relatively homogeneous ecological units until recently. Various authors suggest that understanding boundaries may have an important role in the early detection of global climate change [66–70] and in conservation works [71–74].

Ecotones are also referred to as transition zones, junction zones, tension belts, edges, borders, etc. Ecotones can be considered as the edge or the periphery of an ecological system or as a transient zone between two or more adjoining ecological units. Ecological boundaries which have sharp environmental and ecological gradients are usually unstable [75]. They share common traits with the adjoining regions but also hold unique features [76]. Ecotones promote high biodiversity and unique, rare, specialized, vulnerable species, which make them biodiversity hot spots [74] and may be central regions for future conservation efforts.

Ecotones harbor range-restricted species which are mostly considered to be vulnerable to climatic changes and fragmentation and thus prone to extinction. According to researchers, specialists will be the first to extinct under the sixth mass extinction. The role of specialists prior to extinction processes has a main priority in most studies as they can be used as early warning signals. Generalists as the main survivors of environmental changes are usually disregarded in approaching havocs, though they maintain the communities as well. Kark and van Rensburg [74] argue that not only ecotones but also core regions are threatened by global changes.

Kark and van Rensburg [74] raised an important research question related to ecotonal species assemblage: “Are they young species currently diverging in the ecotone region via parapatric speciation or rather wide-ranging species that have expanded their ranges to ecotonal

environments?" Studies are controversial in this respect, and they emphasize the importance of both generalist and specialist species in core regions and in boundary regions as well.

5.1. Generalized and specialized species in ecotones

In literature, wide-ranging species are implied to in many ways, such as generalist, generalized, widespread, abundant, r-strategist, weed, ruderal, tolerant, invasive, opportunistic, pioneer, and widely dispersing. Narrow-ranging species are referred to as range restricted, narrowly adapted, specialist, k-strategist, competitive, endemic, rare, unique, vulnerable, sensitive, etc. Generalized species are able to adapt to a broad variety of environmental conditions, and they can shift their diet. Specialists are less flexible in adaptation, and they occupy only a narrow range of niche.

Gosz [77] suggests that edge species are likely to be generalist, wide-ranging, and dominant. Generalists are able to cross boundaries. Wide-ranging, generalist taxa are more mobile than sensitive, vulnerable taxa which tend to be sessile; that's why generalists perceive fewer boundaries and detect the landscape more homogenous [78, 79]. Generalist can be forced to leave their habitat and cross boundaries by habitat destruction or overpopulation. For instance, wide-ranging predators leave overpopulated habitat patches and cross the boundaries in cross-edge spillover predation [80–82].

Some studies suggest that generalists might have an important role both in core regions and at boundaries by maintaining communities. For example, krill have an important role in connecting different trophic levels in oceans. They are widespread globally; however, Antarctic krill occur only along the boundary between sea ice and ocean water, because they can find both rich food and shelter from predators there [83].

According to traditional textbooks, specialized species tend to become rare or even lost in a deteriorated environment. In contrast, generalist species prefer impaired habitats where they are found in great number. Disturbed and damaged sites are occupied by generalist species adopting disturbance strategy. However, ecotones can be under disturbance, still having lots of specialized species, and damaged tropical grasslands are rich in specialists as well.

Others studies suggest that the unique environmental conditions favor specialized and endemic species in ecotones [71, 84].

According to Morelli [85], both specialists and generalists should be applied as bioindicators in disturbed landscapes because of the homogenization of communities. He used bird observation data to identify avian hot spots. He selected specialized species in natural environments and both generalized and specialized species in disturbed environments. The selected species varied in different environments. He found that only a few common species are enough to detect high species richness hot spots. He also observed that two specialized bioindicators occurred both in cultivated and natural landscapes (in forest and in grassland, respectively).

McKinney [33] points out that extinction promoting traits tend to covary. According to Brown's hypothesis [86], species having narrow niche are adapted narrowly in several parameters, whereas species with broader niche are broadly adapted in not only one but several

parameters. Furthermore, narrow niche is characterized by low local abundance and small geographical range [87, 88]. Considering the synergistic combination of traits related to narrow niche, the fate of specialist species is sealed under anthropogenic threats [87, 88].

Generalists are usually broadly adapted in not only one but several parameters, while specialists are narrowly adapted in many respects [87, 88] so they represent two extremes of adaptation and thus two extremes of extinction proneness. However, it is important to note that the degree of specialization and generalization can urge or delay extinction processes in the transition zones and in the core regions as well.

Broadly adapted biotas are able to shift their ranges in response to climatic changes [89]. Biotas which are broadly adapted can keep pace with global warming more easily and may experience lower rate of extinction. Several paleontological records confirm the extinction resistance traits of generalist species [90–92]. Generalist species are more resistant to background and mass extinction than specialist ones. Mammals are more specialized than insects, and small mammals are more generalized than large mammals [93]. Scheffers et al. [55] evaluated literature on climate change impacts. They concluded that warming climate may result in a decreased body size in most cases as a large surface-to-volume ratio is more favorable under warm climate [94].

Despite the long history of ecotone investigations [63, 65], studies show mixed results on the role of transition zones in maintaining high diversity [95]. Odum [76] suggested among the first ones that ecotones may have high species richness and unique, endemic species. Since then, several studies seem to have confirmed that near ecotones, species richness and rarity are increased. Kark and van Rensburg [74] claim that boundary regions sustain high diversity because of the adjoinings and overlapping ecoregions (mass effect), but they are also locations for speciation and hence rare and unique species. Kark et al. [95] found that passerine birds, including rare species, occur in higher number in transition zones than in the adjacent ecoregions in the New World. van Rensburg et al. [96] concluded that range-restricted birds and frogs are frequently located closer to ecotones in South Africa. Kark [95] pointed out that rainforest ecotones in Central Africa may be the centers of speciation as a result of evolutionary and ecological processes, hence supporting the biodiversity of the whole biome. Kark et al. [97, 98] observed a biodiversity hot spot at a sharp ecotone between the Mediterranean and semi-arid regions in southern Israel. It is important to note that rarity is one of the best predictors of extinction [33, 91, 99].

Biogeographic regions with the significant level of biodiversity and high rate of endangered species are considered as biodiversity hot spots. It is an interesting question if biodiversity hot spots are ecotonal or rather core regions. The tropical zone is the most abundant of biodiversity hot spots. It has approximately ten times more biodiversity hot spots than the non-tropical zones do [100]. Stevens [101] claims that tropical species are generally more endemic and smaller and they have narrower ranges than temperate species, which make them extinction prone. This might suggest that in the tropical zone both core areas and ecotones have an important role in maintaining biodiversity. Several studies suggest that future extinction will affect the humid tropics the most severely [102, 103].

Tropical grasslands are also diverse and rich in endemic species, and they are as endangered as forests. Grassy biomes include biodiversity hot spots with lots of endemic species. Non-forest habitats are rich in endemic vertebrates and invertebrates. Non-forests hold 30–50% of plant diversity [104]. Ancient grasslands which are alternative stable states of forests are probably rich in endemic species. For example, Cerrado tropical grassy biome in Brazil is a threatened biodiversity hot spot [105].

High rainfall grasslands in Brazil [106], Africa [107], Thailand [108], etc. have a particularly high level of plant diversity and many endemic species. The Indian montane grasslands have many endemic species [109]. Madagascan grasslands are also rich in endemics [110, 111].

Grassy biomes have high light requirements and disturbance tolerance. The similar may be true for sharp boundaries between tropical grasslands and forests. These boundaries are maintained by megaherbivores and fires. High diversity and high number of specialized (and endemic) species are typical for grasslands. Open savannas labeled as “disturbed” or “degraded” harbor many specialists and maintain high diversity in Madagascar and Indonesia [104]. Grassland fauna resists to fire and has great resilience. Savanna species are usually competitive, are mobile, and have a wide range of diet, which means that they can shift their diet, and they prefer open environments [112]. Bond and Parr [104] allege that the loss of grassland specialist birds can be used as early warning signals of shifts to forest at landscape scale considering their large habitat requirements. According to Skowno and Bond [113], specialized bird species of different levels of forest already appeared in significant number in grassy ecosystems.

According to Strayer et al. [114], species assemblage and interactions along boundaries may be unique, or they may represent the average of the adjacent patches. They refer to these two types as “interactive and noninteractive boundaries.” Under certain circumstances, ecotones may be unique environments separately from the adjoining communities and not the mix of the adjacent environments.

5.2. Ecotones and climate change

The Earth’s climate can be characterized by natural cycles of cooling and warming phases. Cooling usually results in less diverse and broadly adapted biotas with selectively eliminated tropical biotas. Warming is beneficial for the development of more complex and specialized biotas [91]. Currently, we are in a controversial situation. Despite the fact that we are undergoing a natural cooling process lowering the diversity level, we are experiencing anthropogenic global warming, which also contributes to extinctions because of its high rate.

The role of ecotones in climate change processes is unclear. Gaston et al. [115] suggest that ecotones are sensitive to global warming as ecotonal species are already at the edge of their ranges, which make them prone to extinctions. Others argue that ecotones are places of temporal and spatial fluctuations; hence, ecotonal communities should be more resistant to global warming [74]. Some also suggest that changes in ecotones might serve as early warning signals of ecosystem shifts [50, 51]. Ecotones may be viable areas that sustain themselves over

time, or they are temporary product of constant flow from the adjacent communities [116]. This might have an effect on their persistence to future global changes.

5.2.1. Importance of ecotones in mass extinction

Conservation works have shifted from protecting of individuals to identifying regions with high diversity [117]: botanical hot spots [118] and hot spots of endemic birds [119], which are targets of mass extinction as rare species are concentrated in small areas. We can assume that a part of the biodiversity hot spots might be transition zones, some of which are rich in young and novel species. Brooks and McLennan [120] and Erwin [121] propose that these regions will be the first victims of mass extinction as they contain restricted-range species in small place so they can be wiped out completely. On the other hand, they might be also the centers of repopulation after mass extinction.

5.2.2. Low latitude ecotones as future refugia

Hampe and Petit [122] suggest that southern (rear) edge of species ranges should deserve greater attention or at least should not be neglected compared to the more studied northern (poleward) expanding edge, as the rear-edge populations store the species' genetic diversity. This might be applied as analogue in case of greater transition zones serving as biodiversity hot spots. It is an interesting question whether low latitude transitional zones are the most important biodiversity hot spots serving as a refugium in future mass extinction.

Based on the estimation of the Late Quaternary glacial-interglacial climate displacement rate, Sandel et al. [123] concluded that high-velocity and unstable regions tend to have mainly widespread species which are resilient to climatic oscillations and have strong dispersal abilities. Their results show that during the Late Quaternary the northeastern part of North America and the north-central Eurasia had the highest velocity and the weakly dispersing amphibians were affected the most. They pointed out that low-velocity regions can be refuges for sessile and small-ranged species [123]. Many bird and mammal endemic species are concentrated in the Southern Hemisphere where a higher velocity of changes can be expected according to predictions [123].

6. Discussion

Biogeographical boundaries are shifting globally. Late Quaternary glacial-interglacial climate change proves that climate displacement rate tends to vary regionally [123]. Sandel et al. [123] argues that high-velocity and unstable regions have mainly widespread species which are resilient to climatic oscillations and have strong dispersal abilities. However, the rapid expansion of specialized species has been observed in the tropical, temperate, and arctic zone as well as in the mountains [1, 55]. Warming climate seems to favor species with strong competitive and dispersal abilities. Recent studies [55] suggest that non-sessile specialized species

which are strong competitors thrive in high-velocity, shifting boundary regions and as Brown and Lomolino [1] conclude that they start to behave as generalists. Other studies describe the extinction of both active- and passive-dispersing specialized species [32]. Short-lived pollinators and birds, for instance, are at great risk.

According to Sandel et al. [123], low latitude transitional zones harbor sessile, small-ranged species and can be characterized by low climate displacement rate. He suggests that low-velocity regions might serve as refuges under anthropogenic extinction processes. Sandel et al. [123] predict that the climate displacement rate will be higher in the Southern Hemisphere than it was during the Late Quaternary climate change. The Southern Hemisphere is rich in endemic hot spots, which suggests a higher rate of endangerment and biodiversity loss. It can also mean that regions which could serve as refugia might be exterminated. Tropical grassland and forest biomes and their boundary regions maintain high diversity and rich in endemic species; therefore, they are jeopardized by global warming.

Several studies pointed out that some ecotones are biodiversity hot spots and they are places for speciation. These observations originate mainly from the tropical and subtropical zones [72, 95]. The core regions harbor specialized species as well. This raises important questions. What are the roles of core region and boundary specialists in extinctions and how much they differ (if they differ) in extinction proneness? Many studies claim that specialization is one of the greatest extinction risks [33], which makes specialized species good bioindicators. Can core region specialists expand their ranges under global warming or they are among the first victims because of the weakening core regions? As nothing is black and white, maybe no obvious answer exists. Local and regional divergences as well as the synergy of many factors suggest several outcomes. For example, African megaherbivores are considered to be specialized in diet. However, recent studies [124] show that they can shift their diet, which makes them more generalized than previously thought. Still, they are endangered boundary species mainly because of overhunting and habitat destruction. Their large body size and higher tropic level also contribute to extinction proneness.

Some studies [77] claim that generalized species might be the beneficiaries of climate change as they are more adaptive than specialized species. However, specialists are displacing generalized species which are supposed to be weaker competitors in many places. Native super-generalists are being expelled by invasive super-generalists in mutualist networks. The decay of generalized species is a threatening issue, because they maintain communities. Fragmentation is a key contributor of their decline in many cases. The increasing number of perishing specialized and generalized species probably refers to a post-initial phase of mass extinction. Morelli [85] suggests the use of both specialists and generalists as bioindicators in deteriorated regions.

Zhu et al. [34] and others observed woody encroachment in many regions all over the world, which might suggest that it helps maintain biodiversity. However, it jeopardizes grassland biodiversity hot spots. Even degraded tropical grasslands harbor several rare, endemic, specialized species. Fragmentation and fewer numbers of natural fires also contribute to the decay of grasslands. At the same time, tropical forests, paradoxically, are also suffering. Extreme

perturbations affect not only boundary but also core regions, which can trigger the invasion of exotic species and the extinction of native species. Climate change-induced woody encroachment is not necessarily accompanied by an increase in biodiversity. On the contrary, biodiversity loss is detected worldwide.

In summary, climate change affects most levels of the global ecosystem. Both core regions and boundaries are eroding which leads to biodiversity loss and homogenization. Decaying generalized species probably refer to a post-initial stage of mass extinction.

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