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Pure and Applied Biogeography

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PURE AND APPLIED BIOGEOGRAPHY

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Contents

Preface

This book—*Pure and Applied Biogeography*—gives a very interesting report and overview about the frontiers of such parts of recent biogeographical research, which plays important roles in solving our most pressing global problems (biodiversity crisis, climate change, water issues, and sustainable agriculture).

Our book consists of three sections: "Introduction", "Pure Biogeography and Global Patterns" and "Applied Biogeography and Regional Issues."

After the introductory chapter, which is about the main branches and aims of biogeography in service of solving global problems, we can find three chapters as parts of the first section.

The first chapter in this section is in close relation with the origin of biodiversity and conservation. The second and third chapters are about the biogeographical aspects of climate change and biodiversity.

In the second section of this book, three applied biogeographical chapters can be found, which are related to agriculture, theoretical background of biological plant protection against herbivores, and regional patterns in ecological biogeography.

I am sure that this book will be very useful for everybody—researchers, professors, students, or others interested in the field—who would like to get an overview about the most practical results and research areas of biogeography nowadays.

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Section 1

Introduction

scientific research. This way we can develop a sustainable global society in a healthy environment and rich biosphere.

In solving our global problems, biogeographical research plays a key role in four main areas:

- Origin and protection of biodiversity
- Global climate change issues
- Water issues, aquatic ecosystems
- Sustainable agriculture, biological pest control issues

2. Biodiversity

In the maintenance and conservation of our planet's biodiversity, knowledge of current biogeographical patterns [23], Earth-historical changes [24, 25], and speciation processes [26] have outstanding importance. Many areas of biodiversity are still completely undiscovered nowadays [27].

The ecological effects of global climate change also have a significant impact on biodiversity, flora and fauna, through biogeographical patterns [28–31].

In the field of nature conservation, a fundamental change of paradigm became necessary due to climate change. The previously dominant "in situ conservation," which is to preserve existing ecological conditions in present habitats, is not always a realistic goal. Consideration should be given to active "eco-engineering" interventions that support the spatial shifts of natural communities as adaptation options. In this, the biogeographic knowledge and the identification of climate-analogous areas could have great importance. It is obvious that such studies should combine analyses of current and Earth-historical biogeographic patterns with climatic scenario-based predictions.

In the biogeographical research on biodiversity, the following key issues can be identified:

- Tropical rainforests, coral reefs, and other biodiversity hotspots
- Natural and near-natural habitats
- Human-influenced habitats and invasions
- Cross-border phenomena
- Paleobiogeography of biodiversity
- Conservation biogeography
- Biogeography of ecosystem services
- Applied biogeographical research in service of sustainable agriculture and organic farming

3. Climate change

Climate change—in close connection with overpopulation, global species extinction and biodiversity crisis, and social crises—is the biggest challenge for mankind in our history. An adequate and stable global climate system is the most basic living condition of the biosphere, and as a part of it, human society and even all other living conditions are dependent on climate. This climatic system also determines the basic biogeographic patterns of our Earth. The fact and the anthropogenic origin of climate change are supported by evidence of a multitude of research findings and observations. With regard to these two things, there is an unprecedented degree of consensus in the scientific world.

In the background of this phenomenon, there are a lot of causes in strict connection with each other like overpopulation of mankind, the fossil fuel production and burning since the industrial revolution, the rapid eradication of forests and natural wetlands, industrial and transport pollution, unsustainable agricultural practices, and the rapid urbanization. Human activity is causing the greatest damage and dangers by breaking down the healthy functioning and regulatory capacity of the Earth's biosphere, eradicating primeval forests and rainforests, draining bogs and swamps, and reducing forest cover. The importance of grazing is also well known in the diversity of nature or near-nature grasslands [32].

There are a number of well-founded and less well-founded opinions about climate change today, but there are some important points that are beyond dispute:

1. The climate determines the living conditions of ecosystems and, at the same time, human society, which are also reflected in large-scale biogeographical patterns.
2. Past climate changes have always had significant ecological impacts, mass extinction of species, new species becoming dominant, and a fundamental change in landscape.
3. The history of the Earth shows a great deal of climate changes, so it must be our basic attitude that, because climate is variable, it changes and the biogeographical and social consequences can be very serious if we are not prepared for them.
4. A better understanding of the relationship between climate and biosphere should be seen as one of our most important research tasks because the existence and prosperity of humanity depend on it.
5. Today, it has become an undeniable fact that the collective activity of mankind is a decisive field-altering, environment-changing factor of our planet, which, besides everything else, also has a significant impact on climate.
6. In our time, global crisis phenomena (biodiversity crisis, raw material and energy problems, consequences of overpopulation and climate change) interact with one another in a synergistic way.

Natural ecosystems provide carbon dioxide binding and storing functions, feedback processes, and in a number of direct and indirect ways regulate the climate in a biogeographical scale, and provide retention and dispensing of leaking residues, as well as the development of favorable micro- and mesoclimate. More recently, it has come to light that seaweeds emit dimethyl sulfide [33] and some pine trees emit terpenes from themselves [34, 47] as a result of rising temperature and carbon dioxide level; these can effectively promote cloud formation and so cool our planet. In addition, there are probably many ecological phenomena and processes so far unknown to science that have a prominent role in the biological regulation of climate [35] and which could also help the survival of the civilization of mankind if we understood and recognized them in time.

In the biogeographical research on global climate change, the following key issues can be identified:

- Climate control potential of different biogeographical units
- The impact of climate change on different biogeographical units
- The role of climate in spatial and temporal biogeographical boundaries and ecological collapses
- Range and time shifts in biogeographical units
- Paleobiogeographical aspects of Earth-historical climate patterns

4. Water and aquatic habitats

Aquatic ecosystems were, for a long time, a neglected area of biogeography, though more than 70% of our planet is covered with water. Water is the foundation of all earthly life, plays a key role in climate change and spatial-temporal patterns of biodiversity, and decisively defines human activity and the possibilities of agriculture.

Climate change and biodiversity crisis issues have a particularly large impact on water, aquatic ecosystems and wet habitats such as oceanic biotopes [36], surface freshwater [37, 38], or groundwater [39]. The state of river water vegetation also has a fundamental effect on animal communities [40].

In the biogeographical research on hydrobiology, the following key issues can be identified:

- Biogeography of oceans and marine habitats
- Biogeography of freshwater habitats and wetlands
- Applied ecogeography of water resources and soil types
- Dynamic biogeography, invasions, and mix-up of communities

5. Sustainable agriculture

The creation of a sustainable and adaptable agriculture is not merely a technological issue, but it is necessary to rethink the whole natural and socioeconomic system related to agriculture from biological, geographical, and human ecological approaches [41].

Sustainable agriculture means a production system where

- The productivity of the agricultural area does not decrease.
- The production does not lead to an increase in the environmental load.
- Soil, air, and natural waters do not get polluted (exceeding their degree of ecological self-purification).
- Soil does not erode.
- Greenhouse gases do not exceed the amount of absorbed quantity during production.
- The quantity and quality (nutritional value and safety) of products produced satisfy social needs.
- The living standards of the family of farmers are ensured.
- Nonagricultural habitats and global biodiversity are also ensured.

The presently dominant conventional agriculture is obviously unable to meet these conditions as agriculture [42]

- is a major source of anthropogenic climate change,
- is a major source of environmental pollution, while
- the productivity of agricultural lands can only be sustained through higher and higher external material and energy inputs (i.e., unsustainable in itself).

For the development of sustainable agricultural systems, only the “high technology” of agriculture is capable: the organic farming sensu lato. This includes organic farming, permaculture, agroforestry, and biodynamic farming.

The productivity, ecological efficiency, and cost-effectiveness of organic farming would be very high (much better than in conventional production) if all of these indicators were to be applied to the unit’s environmental use and environmental load.

The global human population boom and at the same time environmental pollution, damaging nature, and land use pose new challenges to agriculture in the field of sustainability and especially organic farming [43]. In this context, the biogeographical researches affect the cultivated plants, weeds, animal pests and pathogens, and their natural enemies [44], as well as the traditional ecological knowledge [45].

In the applied biogeographical research on agriculture, the following key issues can be identified:

- Anthropogenic changes in biogeography, mix-up of flora and fauna [46]
- Biogeography of grown plants, domestic animals, and their potential genetic resources

- Biogeography of weeds, pests and pathogens, and their natural enemies
- Biogeography of soils and soil biological communities
- Ecogeography of climatic patterns in a changing world
- Biogeographical aspects of agroforestry, organic farming, and sustainable agriculture
- Ethnogeographical aspects of traditional ecological knowledge

Ecological and biogeographical research of natural, near-natural, and human-influenced ecosystems has strategic importance in the struggle for survival of mankind and the chance to create a sustainable society.

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Section 2

Pure Biogeography and Global Patterns

Chapter 2

Are Historical Biogeographical Events Able to Promote Biological Diversification?

Julián A. Velasco

Additional information is available at the end of the chapter

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Abstract

One of the goals of evolutionary biology is understanding how biological diversification change across spatial and temporal scales. Theoretically, it has been established that external (i.e., dispersals) and internal (i.e., origin of a key innovations) factors can modulate shifts in rates of species diversification. However, the role of historical events as trigger of species diversification rates have not been well understood in empirical studies. I reviewed the literature linking historical biogeographic events and species diversification in many groups. Many of studies conclude that dispersals can be associated with exceptional changes in species diversification rates in insular and mainland areas. I discuss the limitations of some approaches used to discover the link between historical biogeography and macroevolution. I propose some predictions under biogeographic scenarios to gain understanding in how historical events promote biological diversification. I suggest that future studies linking biogeography and macroevolution should incorporate ecologically-relevant traits to discern the mechanisms underlying these historical associations. Although new developments in phylogenetic comparative methods have been done, still is necessary more traditional field-based ecological and evolutionary research. The link between biogeography and diversification still remains narrative and a comprehensive approach is necessary to establish how diversification was triggered by historical events.

Keywords: dispersal, vicariance, ecological opportunity, macroevolution, event-based biogeography

1. Introduction

One the main goals of evolutionary biology is to understand why lineages exhibit differences in species diversification, understood as the difference between speciation and extinction rates in a clade. Three competing hypotheses explain differences in species between clades and geographic regions [10, 51, 69]. The first hypothesis, known as the unbounded hypothesis, proposes that speciation and extinction processes are controlled only by time and diversity is not limited by any ecological process [69]. The second hypothesis, known as the bounded hypothesis, states that diversity reaches a limit imposed by the number of competing coexisting species [51, 52]. And a third recently proposed hypothesis, known as the damped hypothesis [10], states that diversity increases without limit and ecological factors constrain speciation and extinction rates.

The understanding of the historical and ecological circumstances where diversification dynamics occur is key to establish whether diversity is limited or not. Therefore, historical events as dispersals can be associated with shifts in species diversification [40]. However, the mechanisms underlying this association remains elusive for many taxa. For instance, for plant clade Dipsacales, it was found that some increases in species diversification rates were associated with dispersal to new geographic areas [40, 41]. Similarly, in Caribbean Anole lizards, it was found that diversification increases occurred after a lineage colonized an island above a certain island size [30, 50]. These two examples show how diversification dynamics can be linked with historical events and suggest also that macroevolutionary dynamics should be explicitly tested in a historical biogeography context.

With the aim to have a comprehensive understanding of the link between historical biogeography and species diversification, it is necessary to consider which ecological or evolutionary mechanisms were involved in this association. Ecological mechanisms can explain how diversification dynamics take place in a region after a biogeographical event. They also offer a conceptual bridge between historical and ecological biogeography. I assert that historical biogeography events (dispersal and vicariance) can promote biological diversification under some specific ecological and evolutionary mechanisms. For instances, some studies have found that some clades diversified through ecological opportunity [28, 33], biotic interactions [63], and/or climate change [26, 65]). The integration of ecological, phylogenetic, and biogeographic approaches in a comprehensive framework is key to understand why some clades diversify extensively when reach some regions and not others.

Here, I conduct a review of studies evaluating the link between biogeographical events and biological diversification. For biogeographical events, I refer mainly to dispersal and vicariance, which have been considered as competing hypotheses in historical biogeography for many years [45, 60]. Dispersal refers to movements of a lineage to a new region across a geographical (or ecological) barrier. Vicariance refers to the fragmentation of an ancestral geographical range and the emergence of geographical (or ecological) barriers. Here, I first discuss how these two biogeographical events can promote shifts in species diversification (e.g., increases in speciation rates or decreases in extinction rates) or diversification dynamics (from time-dependent to density-dependent cladogenesis). Also, I discuss some limitations of methods used to discover this historical link. I establish some basic specific predictions about the expected evolutionary trajectories of ecologically relevant traits under a dispersal or vicariance scenario and how these predictions might be tested using phylogenetic comparative methods. Finally, I provide some possible avenues for an integration of by vicariance [38], it is still unknown whether the emergence of geographical barriers promoted habitat and reproductive isolation in taxa examined. For instance, rapid Andean uplift during the Miocene, with the concomitant climate changes, likely promoted allopatric speciation in *Heliotropium* plant lineages, which adapted to new arid conditions in southern South America [31]. Similarly, the Miocene uplift of the Qinghai-Tibetan plateau promoted allopatric speciation in Asteraceae clades plants [27] and *Rheum* plants [66]. These two clades of plants evolved as a response of temperature changes and the apparition of dry habitat conditions. It is likely that climate changes facilitated bursts of diversification [19, 27, 66]. Again, although these studies show an association between vicariance and species diversification, likely mediated through climate change or emergence of new barriers, it is not clear which mechanisms were involved here. All these studies suggest that we lack the ecological and evolutionary processes in these narrative biogeographic studies and we should look forward to identify at least which main processes underlying these historical associations.

It is evident that dispersal and vicariance events can be associated, either in a narrative or quantitative way, with shifts in species diversification. The link can be inferred directly in some cases [4, 41]; however, again the mechanisms operating behind these events are unknown. Although it is necessary to identify these evolutionary or ecological mechanisms, it is still not clear how these mechanisms can be disentangled. I consider that a full integration of current phylogenetic comparative methods with modern parametrical biogeographical methods and incorporation of ecologically relevant traits might offer new avenues to understand how biodiversity was generated after dispersal or vicariance events.

3.2. Limitations of current methods to link historical events with biological diversification

Some studies only provide a weak evidence of a consistent link between historical biogeographical events and shifts in species diversification rates. In particular, these few studies did not test whether dispersal or vicariance events effectively generated increases in net species diversification rates (e.g., Refs. [4, 7, 9, 68]. For instance, Chaves et al. [9] suggested that Andean uplift promoted increases in species diversification in the *Adelomyia* hummingbird genus. However, they only provide a correlation between divergence times for *Adelomyia* clades with some phases of the Andean uplift. Here, it is necessary to test whether Andean clades diversified more than other clades or the entire group. Accordingly, it is possible to suggest with higher confidence that dispersal to the Andes promoted posterior cladogenesis likely through allopatric speciation.

The link between historical biogeography and species diversification need to be explicitly tested using a two-step framework. First, it is necessary to infer historical biogeographic events with a higher confidence using powerful statistical methods [34]. These methods are ideal to identify rare dispersal events (founder-event speciation; [34]) and allow us to incorporate explicit geological information (e.g., timing of emergence of island landmasses; see Ref. [48] for an example using Caribbean *Anolis* lizards). Many empirical datasets show that founder-event speciation have left a strong imprint on distributional patterns of many taxa [34]. However, it is necessary to develop more complex models allowing the possibility to incorporate life-history traits and how these traits can affect rates of dispersal between regions (e.g., Ref. [35]). After the historical inference is conducted, it is crucial to identify whether these same nodes where a dispersal or vicariance event was inferred exhibit a notable shift in diversification dynamics [2, 3, 66].

Several methods allow to detect specific shifts in diversification dynamics in phylogenies, particularly increases in diversification rates [36, 37, 43, 53, 54]. These methods can be divided into temporal or topological methods, depending on the phylogenetic dataset at hand [43]. These methods also allow us to identify shifts in macroevolutionary regimes (i.e., shifts in diversification process; e.g., bayesian analysis of macroevolutionary mixtures (BAMM) approach developed by [53]; but see Ref. [42] for a criticism about the statistical power). However, these phylogenetic methods are not integrated fully with methods of historical biogeographic inference. Therefore, the association between dispersal or vicariance events and notables shifts in species diversification or diversification dynamics remains narrative [23]. Therefore, new methodologies are necessary to establish with more confidence whether these biogeographical events promote changes in biological diversification. Even more, it is possible that unmeasured traits (e.g., a "hidden" key innovation) affecting speciation and/or extinction rates evolve in the same nodes of a phylogenetic tree where a dispersal or vicariance event was inferred. In these cases, it might be very hard to distinguish whether diversification was affected by the presence (or absence) of a trait or by the movement to a new region (see Ref. [75]).

More robust methods to link historical biogeography and macroevolution are necessary. However, these new phylogenetic methods only can detect these historical associations, but these are very limited to establish the potential ecological or evolutionary process underlying this association. I consider that an integration of ecological studies (including testable predictions of trait-niche evolution) with a historical biogeographic approach will be useful to discern these mechanisms promoting speciation. The association between a biogeographic event and shifts in macroevolutionary dynamics is not enough to understand how biodiversity was generated in many regions. For instance, it has been found in warblers (*Phylloscopus*) that habitat isolation was the first form of niche differentiation to evolve in sympatry, followed by prey-size selection and feeding strategies [74]. It will be important to evaluate whether lineages diversifying after a dispersal event exhibit more niche differentiation [47] than lineages diversifying after a vicariant event. This can help to establish whether the initial trigger of speciation in a lineage was the colonization of a new region and the subsequent habitat isolation in sympatry [12, 13].

3.3. Is it possible to predict some ecological scenarios after a historical biogeographic event?

The ecological and evolutionary processes underlying the historical association between biogeography and diversification have been seldom discussed in the literature. Here, I propose that these contrasting historical events have left different imprints on the lineage diversification of taxa through its evolutionary history.

In a dispersal scenario, some lineages exposed to new ecological conditions (or ecological opportunity) likely experienced rapid diversification and rapid ecological divergence [18, 62, 64, 73]. In these cases, it is assumed that lineages evolved quickly by mechanisms of divergent selection due to ecological release and therefore occurs an increase in species diversification rates with ecological divergence. However, it is still not clear whether

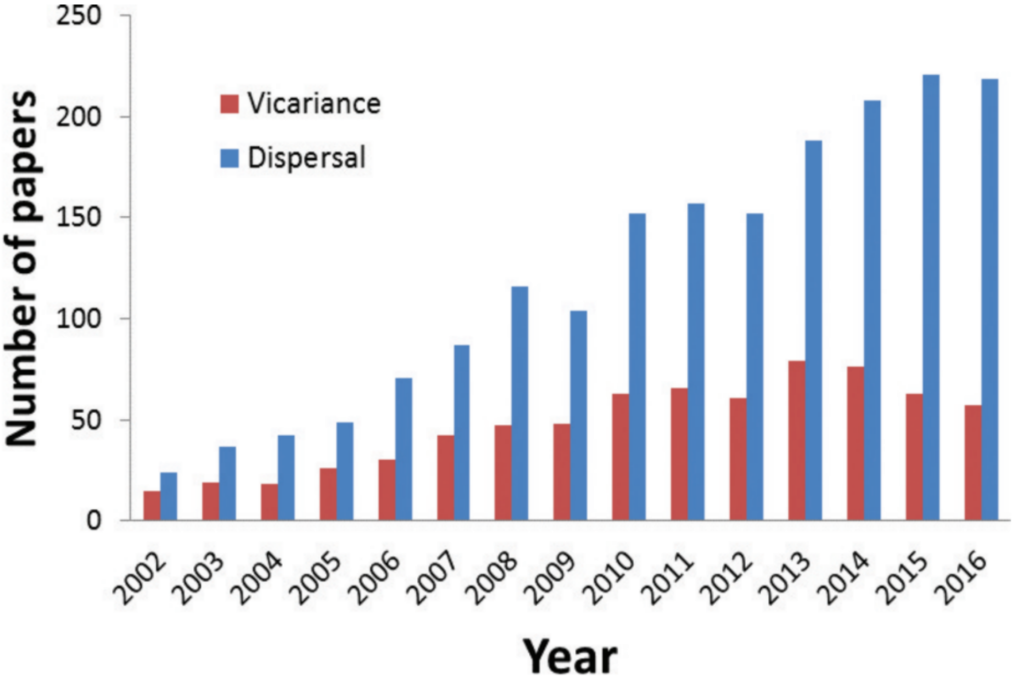

Figure 2. Number of papers published by year identifying dispersal or vicariance events as drivers of species diversification.

ecological or behavioral isolation occurred after the first lineage dispersed to a new region or speciation is driven by vicariance in the new colonized region (e.g., posterior mountain uplift in some islands or regions). Here, it is necessary to test whether a dispersal scenario promotes diversification in a similar fashion and therefore it is crucial to evaluate how species niche-traits evolved after a dispersal event. The colonization of a new region could not be the initial precursor of a change in macroevolutionary dynamics (e.g., increases in speciation rates) and other processes might be obscured here (e.g., reproductive isolation between ecologically diverging subpopulations inhabiting in sympatry [76]) (**Figure 2**).

By contrast, in a vicariance scenario I expected that all species diversification processes occur through allopatric divergence. In this scenario, new species emerge through geographical isolation of populations of a widespread ancestral species [12, 39]. Some studies reviewed here suggest that mountain uplift can generate a spatial gradient of climatic or ecological conditions that promote range subdivision and therefore allopatric speciation [5, 31]. However, still we do not know whether the mechanisms involved here will be different from a dispersal scenario. For instance, it is very well-known that ecological divergence between subpopulations is not a prerequisite for allopatric speciation. Therefore, species might acquire ecological niche differentiation by a pure genetic drift process [6] or species can exhibit strong niche stasis through time [26, 70]. Therefore, to establish whether vicariance effectively promote species diversification, it is crucial to test whether species evolved trait-niches through a pure drift process or maintain ancestral trait-niches due to stabilizing selection [6, 26, 70] (**Figure 2**).

In addition to this, climate change might act as a trigger of species diversification after a dispersal or vicariance event. For instance, many Neotropical diversification have been attributed to quaternary climatic cycles [77], where cooling phases in the Amazon basin facilitated geographic spread of highland species toward lowlands with subsequent range fragmentation and isolation during warm phases [77–79]. In the context of studies linking biogeographical events and diversification, very few studies have been able to detect a positive correlation between past climatic changes and species (or phenotypic) diversification after a given dispersal or vicariance event. For instance, Gamble et al. [80] suggested that main events of cladogenesis in *Gonatodes* geckos coincided with a phase of climate cooling in the late Eocence and Oligocene. In addition, Antonelli et al [81] suggested that speciation in an orchid South American group was accelerated by climate cooling after the Middle Miocene Climatic Optimum, 15 million years ago. However, these two studies did not evaluate whether specific shifts in net diversification rates matched temporally with significant decreases in temperature (i.e., cooling) in each region. Although these two studies suggest that climate change might be a trigger of species diversification, they did not mention how cladogenesis can be affected by climate changes, particularly cooling phases. The link between climate change and diversification is still narrative and more research is necessary to establish first whether there is possibility to find a positive association between both phenomena and then to establish the mechanisms driving speciation by climate change oscillations. For the first part, some recently developed models are able to detect whether paleo-environmental variations (e.g., temperature fluctuations through Cenozoic; [82]) had a significant effect on speciation and extinction rates [43, 83, 84]. These new models allow to establish whether the association is strong and how effectively climate can influence speciation and extinction rates for many groups [85].

Summarizing, both dispersal and vicariance scenarios can promote shifts in net species diversification rates in contrasting ways. In dispersal scenarios, it is expected as an early ecological niche differentiation through the lineage diversification of co-occurring species, as has been the case in Caribbean *Anolis* lizards [29] and Hawaiian spiders [17]. In vicariance scenarios, it is expected, that co-occurring species exhibit ecological niche conservatism in trait-niche axes, either in coarse-grain or fine-grain scales, or that these trait-niches likely evolved by a purely drift process. If ecological niche conservatism prevails after allopatric speciation, it is merely a by-product of the ancestral range fragmentation and therefore it is not possible that it promotes speciation (*contra* [25]). Otherwise, if there is some degree of niche differentiation between species this is likely due to either neutral evolution [6] or adaptation to a slowly changing environment [22]. The distinction between these two patterns (i.e., neutral versus adaptive niche evolution) will be crucial although it can be difficult to be detected using only phylogenetic comparative methods [44]. Furthermore, it is very likely that other ecological or non-ecological processes facilitating speciation occur in each one of these biogeographic scenarios [12]. This suggests that reproductive isolation between subpopulations as by-product of these processes (e.g., polyploidization, hybridization, and genetic drift) is not necessarily driven by historical dispersal or vicariance events. In addition, it is important to remember that inferring an early dispersal event (or vicariance) does not preclude that subsequent cladogenesis occurred by a successive series of vicariance events (or dispersals). For instance, a lineage colonized an oceanic island early in its evolutionary history, but the cladogenetic process that generated *in situ* diversity was driven by successive mountain uplifts.

3.4. Integration of a historical biogeography perspective with modern phylogenetic approaches and ecological studies

An integration of evidence from multiple study fields is necessary to get a deep understanding about the underlying mechanisms of the link between historical biogeography and diversification. Therefore, it will be crucial to develop and integrate new methodological approaches to generate sound evidence of a link between historical biogeographic events and changes in macroevolutionary dynamics. I consider that the first step necessary is to adopt a phylogenetic perspective to study the historical biogeography of a taxa and infer dispersal or vicariance events through its evolutionary history. Many studies reviewed have adopted such perspective, particularly implementing more complex event-based methods [60, 61]. New statistical biogeographical methods incorporating increasingly complex models of range evolution are being developed [34, 58]. The next step is to develop increasingly statistical robust methods to detect shifts in diversification dynamics and evaluate whether these shifts coincide with past dispersal or vicariance events and are not confounded by the emergence of hidden innovation key traits [53, 75]. Although there is a current debate about the power of these methods to detect these shifts [42, 53, 55], the BAMM approach ([53]) seems promising to detect these shifts in diversification dynamics across a phylogenetic tree with high confidence. BAMM allows us not only to detect shifts in speciation rates but shifts in the diversification dynamics itself. For instance, BAMM could allows us to detect in which nodes the diversification dynamics follows a time-dependent process, where only the time for speciation influences speciation rates [69]; or whether it follows a density-dependent cladogenetic process, where the clade diversity is limited by a carrying capacity [51]. Even more, using BAMM we could establish whether a macroevolutionary regime is more prone to occur.

In addition to the statistical detection of these historical association, I suggest that it is necessary to test the specific predictions that might emerge from each biogeographical scenario. I outlined two specific predictions for phenotypic trait evolutionary trajectories after a dispersal or vicariance event (see above). In that case, it is necessary to collect information about ecologically relevant traits for species to test these predictions. This information can be collected from museum specimens (e.g., morphological traits) or field-based studies (e.g., habitat use, diet or foraging strategy). Using model-based phylogenetic comparative methods, it is possible to evaluate whether these traits evolved following a Brownian motion or Ornstein-Uhlenbeck model [20] or whether traits evolved under a pure drift process lacking its phylogenetic signal (e.g., a white-noise process [20]). Furthermore, recently developed methods allow to identify shifts in phenotypic trait diversification in nodes of a phylogenetic tree [14, 15, 53, 59, 67]. In these cases, it is possible to evaluate simultaneously whether specific shifts in species or trait diversification evolved as a response to a dispersal or vicariance event. I consider that testing these predictions allows us to establish potential ecological and evolutionary mechanisms driving biological diversity. Some recent studies have begun to adopt a combination of these new methodologies (e.g., Ref. [24]), but still more research is necessary.

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[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 disturbation 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 CO_2 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.

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

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