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Neotropics as a Cradle for Adaptive Radiations

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Neotropical ecosystems are renowned for numerous examples of adaptive radiation in both plants and animals resulting in high levels of biodiversity and endemism. However, we still lack a comprehensive review of the abiotic and biotic factors that contribute to these adaptive radiations. To fill this gap, we delve into the geological history of the region, including the role

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of tectonic events such as the Andean uplift, the formation of the Isthmus of Panama, and the emergence of the Guiana and Brazilian Shields. We also explore the role of ecological opportunities created by the emergence of new habitats, as well as the role of key innovations, such as novel feeding strategies or reproductive mechanisms. We discuss different examples of adaptive radiation, including classic ones like Darwin's finches and *Anolis* lizards, and more recent ones like bromeliads and lupines. Finally, we propose new examples of adaptive radiations mediated by ecological interactions in their geological context. By doing so, we provide insights into the complex interplay of factors that contributed to the remarkable diversity of life in the Neotropics and highlight the importance of this region in understanding the origins of biodiversity.

"Adaptive radiation," which refers to the proliferation of species occupying diverse ecological niches, has been a well-studied pattern in evolutionary biology since the concept was first introduced by Osborn (1902). The Neotropics is home to several iconic radiations that have played a pivotal role in the development of the theory of evolution and the discovery of natural selection. However, there are several species-rich groups that are either not formally recognized as adaptive radiations or are ambiguously referred to as such (Fig. 1), which highlights the ongoing debate in the scientific community on the very definition of the concept (Givnish 2015). By examining these groups and the ecological and evolutionary factors driving their diversification, we can better understand the role that South American geography, and the neotropics as a whole, played in generating one of the most biologically diverse regions of the planet (Fig. 1).

In this review, we delve into some key patterns and evolutionary mechanisms that are associated with adaptive radiations in plant and animal groups in the Neotropics. Additionally, we identify some new putative examples of unrecognized adaptive radiations for both plants and animals in the region. By examining prominent examples of both adaptive and nonadaptive radiations in the Neotropics, we highlight the importance of geographic features, including geological dynamics, climate shifts, and other historic events, in shaping evolutionary radiations in this region.

While we acknowledge that nonadaptive radiation processes have undoubtedly contributed to the extraordinary neotropical diversity, the processes underlying speciation in nonadaptive radiation do not involve ecologically based divergent natural selection. Moreover, understanding adaptive radiation hinges on two crucial factors: key innovations and ecological opportunities. Key innovations, representing evolutionary breakthroughs, drive diversification by conferring novel advantages. Simultaneously, ecological opportunities arise from untapped niches, fostering rapid speciation. The interplay between these factors propels species into divergent trajectories. By highlighting the roles of key innovations and ecological opportunities, scientists can gain profound insights into the dynamics and patterns of adaptive radiation across taxa and ecosystems.

In this review, we focus on investigating the ecological and evolutionary mechanisms underlying examples of adaptive radiation, shedding light on the diversity, adaptations, and coexistence of species across neotropical habitats.

WHAT DETERMINES ADAPTIVE AND NONADAPTIVE RADIATIONS?

The concept of adaptive radiation has played a fundamental role in understanding the ecological and evolutionary mechanisms underlying the proliferation of species and morphological diversification (Carlquist 1965; Mayr 1970; Stebbins 1974; Martin and Richards 2019; Gillespie et al. 2020). In a broad sense, adaptive radiation is defined as the evolution of ecological and phenotypic diversity in a rapidly diversifying lineage (Schluter 2000). This involves ecologically distinct species with high morphological diversity that allows adaptation to contrasting environ-

Figure 1. The Neotropics and its geographic complexity is a cradle for adaptive radiations. Map of the Neotropical region, spanning from Mesoamerica to central Argentina, including all Caribbean Islands, the Galápagos archipelago, and Juan Fernández islands. The figure shows some of the most iconic examples of animal and plant Neotropical adaptive radiations: (*A*) *Liolaemus*, (*B*) *Philisca*, (*C*) *Anolis*, (*D*) *Geospiza*, (*E*) *Lupinus*, (*F*) *Espeletia*, (*G*) *Scalesia*, (*H*) *Dendroseris*, (*I*) *Robinsonia*. (Photo credits by J. Chaves (*D*), J.E. Guevara-Andino (*E*), Phyllis Coley (*F*), Gonzalo Rivas-Torres (*G*), and D.D. Cotoras (*A*,*B*,*C*,*H*,*I*).)

ments or habitats. It also involves the diversification of multiple lineages from a single common ancestor.

Schluter (2000) proposes four criteria that a group will have to meet to be classified as an example of adaptive radiation. The first criterion is common ancestry, which might or might not involve monophyletic groups. The second implies a correlation between phenotypic diversity and the occupation of novel environments (abiotic and biotic). The third criterion relates to the adaptive advantages of trait expression in their respective environments (trait utility) measured as the trait fitness values compared with the environment. The fourth criterion identifies rapid bursts of diversification for certain groups compared to sister lineages or clades as a characteristic of an adaptive radiation. Finally, some authors suggest a fifth criterion: the coexistence in sympatry of at least three successive sister species (Martin and Richards 2019).

However, it has proven difficult for most studies to fulfill all these criteria, and therefore there are few examples of "true" adaptive radiations (Carlquist 1965; Seehausen 2006; Grant and Grant 2008; Losos 2009; Brawand et al. 2014). Some authors have adopted broader perspectives in which not all of these criteria are met in order to define an adaptive radiation (Givnish 2015; Gillespie et al. 2020). For instance, studies for Darwin's finches and Andean lupines have revealed the role of trait utility, phenotype–environment correlations, rapid bursts of speciation, and common ancestry. However, assuming a rapid burst of speciation as a defining characteristic of adaptive radiation could exclude some of the most iconic examples of adaptive radiations in South America such as the bromeliads of the genus *Brochinnia* (Givnish et al. 2011, 2014).

We do not intend to defend any definition or highlight which lineages qualify as a "true example" of adaptive radiation. Instead, we aim to draw attention to two fundamental elements of this process, ecological opportunity and key innovations (Gillespie et al. 2020). The concept of ecological opportunity as the driving factor in adaptive radiation stems from the early work of Simpson (1953). Ecological opportunity refers to the availability of ecological resources or niche space that were either unoccupied or previously used by competitors (Simpson 1953; Stroud and Losos 2016, De-Kayne et al. 2024). While Simpson (1953) suggested that ecological opportunities emerge from geographic, ecological, and evolutionary access to new niches that collectively determine a new "adaptive zone," the existence of the space by itself does not generate adaptive radiation. Instead, a radiating lineage must gain access to new niches geographically through colonization, ecologically by using resources for which competition is reduced, and evolutionarily by having the adaptations to use such resources in the first place (i.e., enter a new "adaptive zone"; see also Donoghue and Sanderson 2015). Therefore, ecological opportunities are defined by the relationship between lineages and ecological space such that a lineage must gain access across all three dimensions (i.e., geographic, ecological, and evolutionary) to radiate (Simpson 1953; Stroud and Losos 2016). By conferring access to ecological opportunities, "key innovations"—traits that enable lineages to occupy a previously inaccessible ecological state that might promote diversification (Miller et al. 1949; Simpson 1953; Rabosky 2017)—become central to the concept of the adaptive zone. We explore how the evolution of key innovations is related to the occupation of novel niches (i.e., abiotic and biotic ecological opportunities) as the result of the dynamic neotropical geological history.

In contrast to adaptive radiations, nonadaptive radiations have been less studied, as ecological opportunity and adaptive divergence as drivers of diversification might be absent (Schluter 2000; Rabosky 2017). Nonadaptive radiations may show morphological or physiological divergence unrelated to the environment or resource use patterns (Givnish 2015). For instance, the radiation of *Scytalopus* tapaculos among birds and *Phlegmariurus* fir mosses among plants are considered as nonadaptive neotropical radiations (Testo et al. 2019; Cadena et al. 2020). Nonadaptive radiations presuppose rapid lineage diversification despite little-to-no ecological differentiation and usually as the result of allopatric or parapatric speciation (Rundell and Price 2009; Czekanski-Moir and Rundell 2019). Thus, the role of geographic barriers (e.g., lack of gene flow) promoting species formation among populations experiencing similar environments with no influence of divergent natural selection is a basic tenet of nonadaptive radiations. Because new alleles arising in different geographically isolated populations may become fixed or lost depending on population size and the selective advantage of the alleles, nonecological speciation may occur slowly in nonadaptive radiations (Nosil and Flaxman 2010; Czekanski-Moir and Rundell 2019). Nevertheless, nonadaptive radiations triggered by geographical isolation could predate ecological divergence (Losos and Ricklefs 2009; Rundell and Price 2009; Givnish 2015; Gillespie et al. 2020).

ECOLOGICAL OPPORTUNITY AND KEY INNOVATIONS IN THE CONTEXT OF NEOTROPICAL GEOLOGY

The geological history of the Neotropics has directly shaped biodiversity patterns across the continent (Fig. 2; see Box 1 for more details on neotropical geology). The tectonic and volcanic events that triggered the formation of the isthmus of Panamá, the Andean mountains uplift, the formation of the Caribbean islands, and the formation of the Pebas megalake system are just a few examples of the major geological events that created a myriad of habitats and ecosystems throughout the Neotropics (Hoorn et al. 2010; Gutiérrez-García and Vázquez-Domínguez 2013; Pérez-Escobar et al. 2022; Sanín et al. 2022). While the emergence of geographical barriers can promote nonadaptive radiation, we first focus on the role of geological dynamics in adaptive radiation. We outline how these events may shed light on ecological opportunity and ecological release as preconditions for subsequent adaptive radiations.

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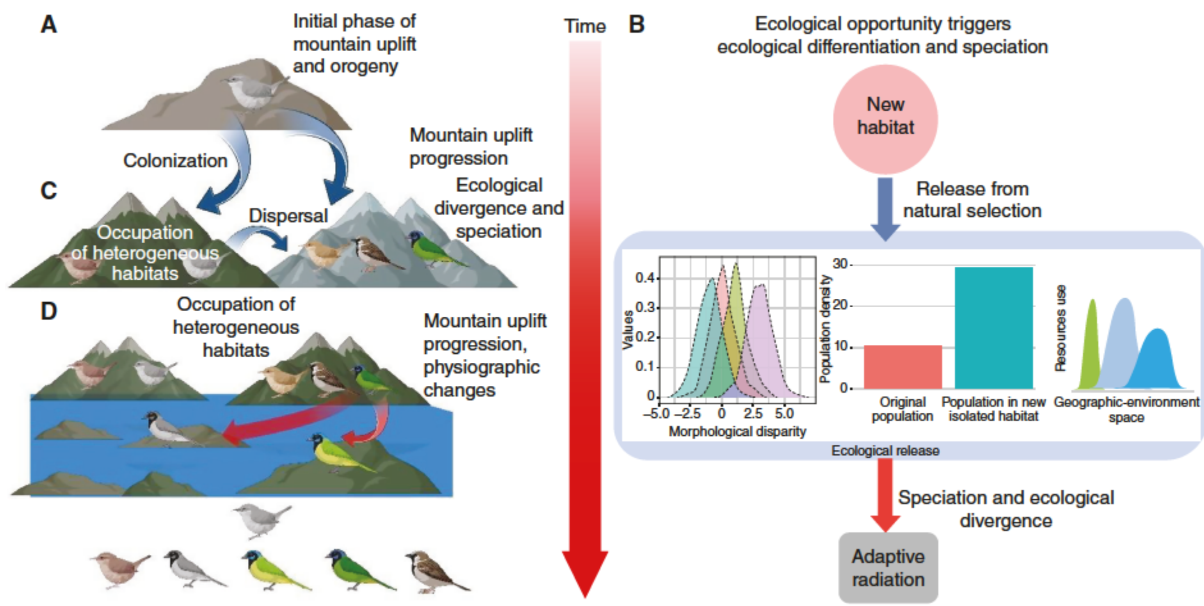

Figure 2. Geological events, in this case mountain orogeny, have a direct impact on adaptive evolution and ecological opportunity. Historical events have played a major role in the origin of biodiversity not just because geological changes can trigger evolution, but also because environmental conditions are the stage on which evolution occurs. However, few attempts have been made to understand the role of geomorphology on adaptive radiation. (*A*) Once plate tectonics is underway, mountain uplift creates the conditions for the formation of new habitats. Interrelatedly, ecological opportunity and ecological release occur after an ancestral lineage disperses to these new unoccupied environments. (*B*) Opportunity and release may act to relax negative selection, promoting lineage and morphological diversification (disparity) through habitat or resource use expansion, an increase in population density, and release from interspecific competition. (*C*) For instance, geomorphological changes during the Andean uplift may have created a myriad of novel environments where previously unused resources became available to new colonizers. Once an ancestral lineage colonizes this new environment, the lack of competition for resources should favor radiation in the multiple available adaptive zones (*D*).

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BOX 1. A BRIEF GEOLOGICAL HISTORY OF THE NEOTROPICS

The Evolution of Western Amazonian Landscapes and the Pebas System

The Andes are the longest mountain range in the world, and its emergence was a major historical event in the evolution of South America's landscape and particularly for Amazonian forests. Since the Cenozoic (~23 myr), the Andean uplift has led to highly heterogeneous habitats by modifying climatic patterns and generating physiographic changes (Hoorn et al. 2010, 2013). During the Paleogene and before the Andean uplift (65–30 myr), the major sources of sedimentary material for the Amazon basin were both the Guiana and the Brazilian Shields, which both formed during the Precambric and were mainly characterized by poor nutrient content and quartzitic sandstone. The flow of sediments was in a westward direction with major depositional basins in the current Central and Western Amazonia. By this time, the proto-Amazon River drainage system was a reverse system completely dissimilar to the current drainage system. The environment of the pan-Amazonian basin during the Paleogene (65–30 myr) was mainly characterized by alternating fluvial conditions and marginal marine embayments (Roddaz et al. 2009; Hoorn et al. 2010). By the early mid-Miocene (23–16 myr), the central and northern portions of the Andes started to uplift creating the conditions for physiographic changes that contributed to the formation of the current Amazon River drainage (Hoorn et al. 2010).

These physiographic changes set the conditions for the simultaneous formation of the Pebas lacustrine system during the middle-late Miocene 29–9 myr (Wesselingh et al. 2006; Roddaz et al. 2009). A drastic reorganization of these landscapes occurred in the early late Miocene, some 8–9 myr. In a short time, fluvial landscapes led by the uplifting Andean hinterland to the west replaced the former Pebasian wetlands and the modern easterly course of the Amazon became established. Fossil evidence of freshwater fauna (e.g., reptiles, fishes) corroborates the evolution of a heterogeneous landscape including freshwater swamps and islands of terra firme-white sand forests in the current Western Amazonia. Marine incursions from the Caribbean Sea through the Llanos system during the Miocene also contributed to the landscape heterogeneity (Alvim et al. 2021).

The Guiana Shield

The geomorphological dynamics of the Guiana Shield is related to the topographic, geological, and hydrological dynamics of the so-called Amazon platform of Proterozoic origin (2.5–1.8 bya). In some regions such as the northern portion of the Amazon platform, Proterozoic outcrops are visible as is the case of Roraima mountain (2810 m) or Pico de Neblina mountain (3014 m). These are the major tepui-like topographic formations in a vast region that comprises ~2,280,000 km^2 (Lujan et al. 2011).

The Brazilian Shield

The Brazilian Shield covers most of the Brazilian territory expanding toward the center of the Andean chain to the west and the Patagonian massif to the south (Hartmann and Delgado 2001). The three major tectonic units are older than 900 myr, and there is evidence of Proterozoic parental material in the eastern portion of Brazil (Hartmann and Delgado 2001). Most of the Brazilian Shield also includes the highlands extending between the central-north portion of the Amazon toward the Rio de la Plata estuary in the south. Little is known about the geomorphological history of the Brazilian Shield and it has been argued that long-term stability tectonics might be responsible for this lack of information. Nonetheless, the eastern margin of the shield has suffered significant tectonic and physiographic changes since the Cenozoic. Some of the most important geological events that shaped the eastern portion of the Brazilian Shield are related to the uplift of mountain ranges along the Atlantic coast of Brazil that have produced a sharp geomorphological contrast between the narrow Atlantic coastal slope and the broad inland (Harrington 1962; Buckup 2011). Two major geological basins characterize the lowland eastern portion of the shield, the Sao Francisco and the Parana River basins. Together these geomorphological characteristics have produced an extremely heterogeneous landscape with several habitats and climatic conditions favoring the diversification of several plant and animal groups.

Continued

Andean Orogeny and the Evolution of the Two "Arid Diagonals" Páramo–Puna–Altiplano Systems

The Andean orogeny is complex and there is still ongoing debate about the pace and time of the evolution of this system. The Andes-Altiplano is one of the largest mountain belt systems in the world extending from ~10°N to 50°S as a consequence of subduction of oceanic lithosphere beneath an initially flat continental margin. The subduction along the Pacific margin originated during the Paleogene (65–34 myr), causing the initial uplift of the Northern and Central Andes (Hoorn et al. 2010; Armijo et al. 2015). However, this is disputed as it has been suggested that the initial stage of the uplift of the northern Andes occurred at ~80 myr (Horton 2018). The limit between the northern and central Andes is defined by the subduction of the Carnegie ridge under the South American plate in Ecuador producing the geomorphological phenomenon known as the Huancabamba depression (Pérez-Escobar et al. 2022). In the northern portion of the Andes, one of the major geological events was the initial uplift of the eastern cordillera that provoked subsequent orographic and climatic changes including the separation of the Orinoco and Magdalena rivers basins (Hoorn et al. 1995; Horton et al. 2010). This process initiated ~26–23 myr and was one of the major physiographic changes that promoted the evolution of habitat heterogeneity at basin scale. The central portion of the Andes, which extends along a 2000 km belt in a NW–SE direction and 3200 km in a N–S direction, began orogenic deformation in the Cretaceous ~70 myr (Horton and DeCelles 1997; Pérez-Escobar et al. 2022). Associated with the Altiplano formation is the existence of a series of high-elevation lakes, of which the one with the current largest size is Lago Titicaca. Those lakes have been strongly affected by changes in precipitation regime during the Pleistocene glaciations, which has resulted in expansions, connections, and droughts of many of them at different times (Horton and DeCelles 1997). In the case of the southern portion of the Andes geological and physiographic changes started ~100 myr, but extreme uplift events that shaped the current conformation began only ~15 myr (Hervé et al. 2000).

Together these orogenic events changed dramatically the climate and physiography of the entire continent creating two "arid diagonals" (Luebert 2021). In the northern and central Andes, uplift increased rainfall in the east and a rain shadow effect with dry conditions in the west of the mountain range, this created the conditions for the evolution of landscapes and habitats in the eastern dry diagonal including the Cerrado, Caatinga, and Chaco biomes (Pérez-Escobar et al. 2022). In the central and southern Andes, the western arid diagonal connects the Atacama desert, Monte, Prepuna, dry Puna, Pampas, and eastern Patagonia. These two diagonals effectively isolate three major humid forest formations in the continent: (1) Amazonia + tropical Andes + Chocó, (2) Mata Atlántica, and (3) Valdivian Jungle.

Continental and Volcanic Islands

South America is surrounded by several volcanic archipelagos and continental islands. Along the Pacific coast from north to south, it is possible to find: Isla Malpelo, the Galápagos archipelago, the Desventuradas islands, and the Juan Fernández archipelago. All of them are over the Nazca plate, which creates a general time chronosequence where the older islands tend to be closer to the continent (Harpp and Geist 2018; Lara et al. 2018). Along the Atlantic coast, also from north to south, it is possible to find: the São Pedro and São Paulo archipelago, the Fernando de Noronha archipelago, and the Trindade e Martim Vaz archipelago. There are also several near-shore continental islands and island formations on the delta of large rivers (e.g., Amazon and Río de la Plata). The area with the highest concentration of them corresponds to the fjords area in southern Chile. Most of them are of glacial origin.

Major geological changes through time in the continental Neotropics often involve mountain uplift and plate tectonics. Uplift during mountain growth is directly related to physiographic modifications including changes in drainage patterns, which in turn could lead to bridges or barriers for species dispersal. Mountain uplift also generates modifications in atmospheric circulation patterns, leading to changes in precipitation regimes. In South America, the Andean orogeny and the emergence of the tepuis formation in Brazilian and Guiana Shield cratons dramatically changed the flow and the direction of sediment deposition for more than 100 myr (Hoorn et al. 2010, 2013; Pérez-Escobar et al. 2022). These changes, along with widespread erosional processes, changes in orographic precipitation, and marine incursions, have resulted in the formation of a highly heterogeneous landscape with multiple opportunities for radiation (Fig. 2).

Although many of the best-documented examples of adaptive radiation in the Neotropics are associated with geological events, we do not suggest that geology alone triggers bursts of speciation and ecological divergence. Instead, we propose that the environmental settings for evolution are necessarily related to historic events involving natural selection. Therefore, geological events have played a major role in the origin of neotropical biodiversity, especially because extrinsic abiotic factors (i.e., geology) such as the emergence or collapse of geological barriers, island formation, or climate variation, can trigger evolutionary processes. Despite several attempts to correlate neotropical geological history to ecological opportunity in the context of adaptive radiation, few examples have explicitly tested the role of the paleoenvironment in diversification and ecological divergence. Thus, we link geological dynamics with ecological opportunity, and key innovations to explain particular plant and animal neotropical adaptive radiations (Fig. 2). In the next sections, we will summarize the most iconic examples of adaptive radiation in both plants and animals and the link between ecological opportunity and neotropical geological history.

Plants

In this section, we describe a few proposed cases of adaptive radiations in neotropical plant groups. However, the paucity of literature on plant adaptive radiations in South America creates a major gap in understanding how geomorphology and climate shape these radiations in the Neotropics. Although multiple studies have focused on documenting bursts of diversification (Meseguer et al. 2022) or the evolution of "key innovations" to enable the colonization and spur the diversification of various plant lineages in new ecological settings (Kadereit and von Hagen 2003; von Hagen and Kadereit 2003), few studies have examined explicitly and experimentally how trait utility and environment to phenotype correlations influence organismal fitness and diversification. Further work is critically needed to link ecological opportunity and adaptive divergence from comparative, populational, and optimality perspectives in the neotropical flora (Kadereit and von Hagen 2003; von Hagen and Kadereit 2003; Olson and Arroyo-Santos 2015).

The most common feature of plant adaptive radiations in the neotropics is the role of South American geological history. From the emergence of the Galapagos archipelago to the intricate geology of the Andes, the Guiana Shield, and the Brazilian Shield, these geological events have created a mosaic of diverse habitats and climatic niches. These factors have significantly contributed to generating ecological opportunities for the adaptive radiations of plants. We synthesize cases of adaptive radiation in neotropical plant groups and summarize the characteristics of the most well-documented cases, including the *Espeletia* complex, lupines, and bromeliads (Table 1). In addition, we present evidence for a new case of a plant adaptive radiation in the genus *Scalesia*, which has not been treated as such in the literature.

Owing to their remarkable ecological and phenotypic diversity, the Scalesia radiation is often likened to the "Darwin's finches of the plant world." Endemic to the Galápagos Islands, *Scalesia* comprises approximately 15 species of trees and shrubs occupying various climates and habitats across 11 islands (Schilling et al. 1994; Itow 1995; Fernández-Mazuecos et al. 2020). Geological dynamics have created extreme habitat heterogeneity, promoting ecological opportunities for speciation and adaptation in *Scalesia* (Geist et al. 2014). Leaf and inflorescence morphology have evolved repeatedly, leading to differentiation in climatic niches and plant–pollinator interactions (Fernández-Mazuecos et al. 2020). Leaf variation in *Scalesia* reflects adaptation to within-island climatic gradients, with smaller-leaved species occupying dry lowland habitats and larger-leaved species thriving in humid uplands (Perez et al. 2023). While the *Scalesia* adaptive radiation is well-established, the genomic basis of adaptive traits remains largely unexplored (Cerca et al. 2023), evidence indicates that the selection of genes associated with climatic niches may drive the adaptive radiation in *Scalesia* (Eliasson 1974; Walter et al. 2016; Fernández-Mazuecos et al. 2020; Cerca et al. 2023; Perez et al. 2023).

Animals

In this section, we describe the better-documented cases of adaptive radiation in neotropical vertebrate groups highlighting recent evidence to propose new cases of adaptive radiation (Table 2). The most iconic examples of vertebrate radiation come from the studies of Caribbean *Anolis* and Darwin's finches. Nonetheless, mounting evidence from phylogenomics, anatomical, paleontological, and functional analyses have shed light in terms of documenting additional examples including neotropical cichlids, as well as multiple mammals and bird lineages (Grant 1986; Grant and Grant 2008; Tebbich et al. 2010; Lamichhaney et al. 2015; Jiménez-Ortega et al. 2023).

The neotropical cichlids (subfamily Cichlinae) include more than 600 species distributed in riverine and lacustrine systems of Central and South America (López-Fernández et al. 2010, 2013; Arbour and López-Fernández 2016). This fish radiation is both morphologically and ecologically diverse, with rampant repeated evolution of specialized feeding strategies (e.g., detrivory, piscivory, substrate sifting) in Central and South America clades (Winemiller et al. 1995; Arbour and López-Fernández 2014, 2016). Variation in rates of evolution of functional feeding morphology is consistent with a scenario of changing ecological opportunity and ecological release operating at different spatial and phylogenetic scales. As an example, colonization of new habitats facilitated by the Panamá Isthmus formation ~3–10 myr (Hulsey et al. 2010) and release from South American competitors promoted bursts of diversification and morphological disparity in Central American lineages (e.g., Geophagus, Acarychthis, Herychthis) (Hulsey et al. 2010; Arbour and López-Fernández 2016).

Numerous instances of diversification and adaptive radiation in tropical birds have been extensively studied, with hummingbirds (family Trochilidae) serving as a prominent example. These nonpasserine birds, comprising approximately 340 species diverging from swifts ~42 myr, exhibit specialization in nectar consumption, leading to intense interspecific competition (Temeles et al. 2009; Martín González et al. 2015). Rapid and variable diversification rates underscore the complexity of hummingbird evolution (McGuire et al. 2014). Hummingbirds have undergone adaptive radiation driven by their expansion into new habitats, particularly in the Andes, recent evidence suggests the adaptive value of genes associated with high-elevation physiological tolerance both between and within species level (Lim et al. 2019, 2021; Barreto et al. 2023). The timing of Andean uplifts, ~6–10 myr and 2–5 myr, facilitated habitat expansion and access to new food resources, contributing to the evolutionary success of hummingbirds (Gregory-Wodzicki 2000; Garzione et al. 2008; Bershaw et al. 2010; McGuire et al. 2014; Lim et al. 2019). Overall, hummingbirds represent one of the most comprehensively studied neotropical adaptive radiations.

ECOLOGICAL OPPORTUNITY AND KEY INNOVATIONS IN THE CONTEXT OF BIOTIC INTERACTIONS

Plant–Herbivore Interactions

It has been long recognized that interspecific competition for resources could drive divergence during adaptive radiations. The classical ecological theory of adaptive radiation states that the last stage in the diversification process should be related to the increased phenotypic divergence of closely related species coexisting in sympatry (Lack 1983; Schluter 2000). This process has been linked to divergence mediated by resource partitioning and increased specialization after speciation, and most of the literature on adaptive radiations has been focused on the role of competition and ecological opportunity

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Table 1. Summary of neotropical plant adaptive radiations highlighting accepted examples and proposing new cases based on current evidence about the role of geology

Adaptive radiation	Clade	Age (myr)	Number of species	Associated geological event	Ecological opportunity	Key innovation(s)	Accepted as adaptive radiation following Schluter (2000)	Key references
Lupines	Lupinus	0.4–1.93	85–90	Final phase of the northern Andean uplift	Appearance of high-altitude cold-humid habitats (paramos, montane forests)	Variation in growth form and perenniality	Yes, but contested by Givnish (2015)	Hughes and Eastwood 2006; Drummond et al. 2012; Hughes and Atchison 2015; Nevado et al. 2016
Espeletia complex	Espeletia	3–5	~140	Final phase of the Andean uplift	Appearance of high-altitude cold habitats (super paramos, high-altitude swamps)	Rosette growth form evolution, reproductive syndromes associated with the type of inflorescence	Yes	Monasterio and Sarmiento 1991; Cuatrecasas 2013; Diazgranados and Barber 2017; Pouchon et al. 2018
Bromieliads	Tillandsioideae	15.1–16.9	~1256	Evolution of the Andes and the Atlantic forests	Creation of new open multiple edaphic and climatic niches	Epiphytism, tank habit, water and soil nutrient absorptive trichomes, the CAM photosynthetic pathway, and avian pollination	Yes	Givnish et al. 2011, 2014; Silvestro et al. 2014; Males 2018
	Bromelioideae (Brazilian Shield clade, Brochinia)	7.5–9.4	753	Emergence of the Brazilian and Guiana Shields	Heterogeneous landscape spanning climatic and edaphic gradients	Epiphytism, tank habit, water and soil nutrient absorptive trichomes, the CAM photosynthetic pathway, and avian pollination	Yes	Givnish et al. 2011, 2014; Silvestro et al. 2014; Males 2018

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Table 1. *Continued*

Adaptive radiation	Clade	Age (myr)	Number of species	Associated geological event	Ecological opportunity	Key innovation(s)	Accepted as adaptive radiation following Schluter (2000)	Key references
	Bromelioideae (Tank clade)	9.4–10.7	629	Emergence of the Brazilian and Guyana Shields and evolution of the Andes	New open multiple edaphic and climatic niche	Epiphytism, tank habit, water and soil nutrient absorptive trichomes, the CAM photosynthetic pathway, and avian pollination	Yes	Givnish et al. 2011, 2014, Silvestro et al. 2014; Males 2018
Darwin giant daisies	Scalesia	0.63–0.74	∼16	Galapagos archipelago geology	New open climatic niches and available pollinators	Leaf dissection, pubescence, and inflorescence morphology	Recently proposed	Itow 1995; Fernández-Mazuecos et al. 2020; Cerca et al. 2023; Perez et al. 2023

Further details of these systems are provided in the text and the Supplemental Information.

Table 2. Summary of neotropical animal adaptive radiations highlighting accepted examples and proposing new cases based on current evidence about the role of geology

Adaptive radiation	Clade	Age (myr)	Number of species	Associated geological event	Ecological opportunity	Key innovation(s)	Accepted as adaptive radiation following Schluter (2000)	Key references
Hummingbirds	Trochilidae	42	363	Andean uplift	Flower nectar	Variability in bill size and shape, body size	Yes	McGuire et al. 2014; Barreto et al. 2023
Tyrant flycatchers	Tyrannidae	~25	>441	Expansion of semi-open and open habitats from mid-Miocene onward	Insects in diverse levels of vegetation clutter	Foraging behavior	Yes, but not tested with recent macroevolutionary techniques	Fitzpatrick 1985; Ohlson et al. 2008
Ovenbirds and woodcreepers	Furnariidae	~25	315	Andean uplift, expansion of semi-open and open habitats, river basin reconfiguration	Insects on trunks and vegetation	Ecomorphological adaptability, nest architecture	Yes	Claramunt 2010; Derryberry et al. 2011
Tanagers	Thraupidae	~12	384	Andean uplift, expansion of semi-open and open habitats	Dietary and habitat niches	Rapid bill shape evolution	Yes	Sedano and Burns 2010; Vinciguerra and Burns 2021
Darwin finches	Geospiza	1.5	14	N/A	New and unused food resources	Beak size and behavioral innovation	Yes	Grant 1986; Grant and Grant 2008, 2016; Tebbich et al. 2010; Lamichhaney et al. 2015; Burress et al. 2021
Liolaemus lizards	Liolaemus	~39	>250	Andean uplift	Cold mountaintops	Viviparity	Yes	Esquerré et al. 2019

Continued

Table 2. *Continued*

Adaptive radiation	Clade	Age (myr)	Number of species	Associated geological event	Ecological opportunity	Key innovation(s)	Accepted as adaptive radiation following Schluter (2000)	Key references
Caribbean Anolis	Anolis	∼43–51	>400	Great Antilles and northern Lesser Antilles geology	Microhabitat differentiation promoted by Caribbean islands emergence	Adhesive toe pads, sexual dimorphism	Yes	Losos et al. 1998; Losos and Ricklefs 2009; Mahler et al. 2010; Huie et al. 2021
Rain frogs	Eleutherodactylus	∼20	>167	N/A	Caribbean islands	Diversity of habitat use	Yes	Jiménez-Ortega et al. 2023
Caribbean pupfishes	Cyprinodon	0.01	∼55	Caribbean islands complex geology, islands formation, and sea level changes	Availability of diverse freshwater habitats	Exceptional craniofacial divergence	Yes	Martin and Wainwright 2013; Martin 2016; Martin et al. 2017
Neotropical cichlids	Cichlinae	∼60	600	N/A	New lacustrine and riverine habitats (e.g., Central America)	Jaw and body size variability	Yes	Arbour and López-Fernández 2016
Platyrrhine monkeys	Platyrrhini	∼25	160	N/A	Diet	Brain shape, face, neurocranium, and body/cranial size	Yes	Aristide et al. 2018
Neotropical leaf-nosed bats	Phyllostomidae	∼30	227	N/A	Nocturnal noninsect diets	Variation in skull shape	Yes	Dumont et al. 2012; Rojas et al. 2018

Further details of these systems are provided in the text and the Supplemental Information.

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as drivers of adaptive diversification (Schluter and McPhail 1992; Grant and Grant 2006). However, other types of ecological interactions including exploitative interactions might be promoting divergence during adaptive radiation (Schluter 2000). Understanding how some types of exploitative interactions, such as predation, could lead to diversification, is fundamental to defining the role of ecological interactions as drivers of adaptive radiations.

One of the most ubiquitous examples of exploitative interactions is the association between plants and their insect herbivore enemies. More than 50 years ago, Ehrlich and Raven's foundational paper proposed that selection by herbivores was central for plant adaptive radiation (Ehrlich and Raven 1964). Specifically, they predicted that after the evolution of a key innovation, in this case, a "new defense" in response to herbivory, plant species would be able to escape and radiate. Similarly, selection would favor counter-adaptations from herbivores to this new defense and ultimately adaptive radiation onto a set of host plants (Ehrlich and Raven 1964). Ehrlich and Raven argued these coevolutionary arms race may explain a substantial fraction of plant and insect diversities. Although enemy-driven adaptive radiation via the evolution of plant defenses was a key prediction from Ehrlich and Raven's (1964) coevolutionary hypothesis, it has remained largely understudied.

Recent advancements in phylogenetic and metabolomic tools are shedding light on the role that plant–herbivore interactions may play in the rapid and adaptive diversification of species-rich groups in Amazon tree lineages. The tree genus Inga (Fabaceae) exhibits the highest diversification rates in the Amazonian tree flora with more than 300 species (Richardson et al. 2001). Inga has rapidly radiated over the past 4–8 myr, displaying remarkable levels of sympatry with more than 40 species coexisting at a single site (Richardson et al. 2001; Valencia et al. 2004; Nicholls et al. 2015). Despite similar resource use, pollination, and dispersal traits (Koptur 1983; Pennington et al. 1997), divergence in defenses enables high congeneric coexistence, with co-occurring species being more dissimilar in defenses than expected by chance (Kursar et al. 2009; Forrister et al. 2019; Endara et al. 2022). This is consistent with the idea that rapid evolutionary change is likely due to selection by herbivores (Kursar et al. 2009; Forrister et al. 2023).

Despite the consequences that multiple defensive niche dimensions have on fitness and adaptation, these differences have not been tested experimentally in *Inga*. Evidence suggests that different defensive traits (i.e., chemistry, developmental defenses, physical defenses) have diverse functions and evolve independently providing numerous niche dimensions, potentially driving speciation and adaptation in *Inga* (Coley and Kursar 2014; Endara et al. 2017). Empirical observations suggest that divergence in chemical defensive traits in populations of *Inga leiocalycina* in contrasting environments might be related to increased fitness (MJ Endara et al. unpubl.). Furthermore, feeding choice experiments and field surveys of sawfly larvae among populations of the *Inga capitata* complex in Peru showed that differences in chemical defenses are related to fitness when combined with asymmetries in other defensive axes (e.g., developmental, phenological) (Endara et al. 2015). Current evidence suggests that there might be two specific mechanisms operating on the evolution of adaptive chemical defensive traits in *Inga* (Endara et al. 2023; Forrister et al. 2023). The evolution of novel chemicals to escape from herbivores may be the result of gene duplication and neofunctionalization of sets of genes previously involved in a specific metabolic pathway to produce a chemical compound and compound classes (Lego chemistry scenario). These key innovations may open new adaptive zones for those lineages that have evolved such chemical defenses (Fig. 3).

Comparative evidence suggests the evolution of L-tyrosine, a primary metabolite overexpressed in the expanding leaves of *Inga*, might be a key innovation. This chemical compound, highly toxic for generalist herbivores at concentrations from 5% to 20%, evolved once in *Inga* ~4.7 myr in a clade comprising 21 species (Lokvam et al. 2006; Coley et al. 2019). Thus, the overexpression of this chemical compound class may have allowed the ancestor of the L-tyrosine clade to enter a new enemy-free space adaptive

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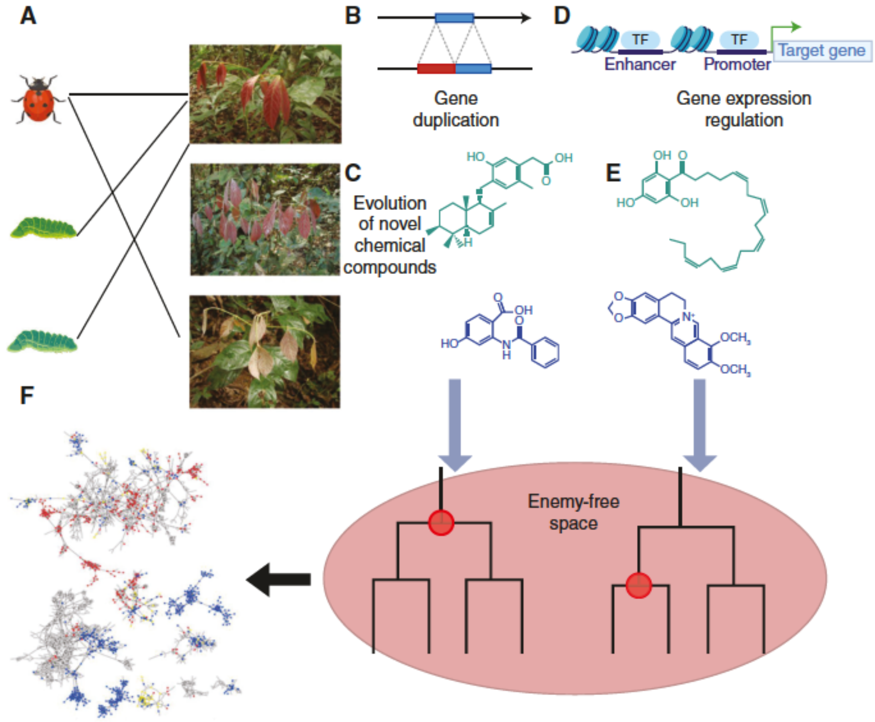

Figure 3. Conceptual framework for plant–herbivore mediated adaptive radiation in the neotropical tree genus *Inga*. (*A*) Selective pressure from herbivores promotes the evolution of chemical defenses to counterbalance the effects of herbivory on plant fitness. In the case of the neotropical genus *Inga* two main genetic mechanisms are proposed to be involved in the evolution of chemical defenses and subsequent radiation of host plants. (*B*) Duplication and subsequent neofunctionalization of specific genes involved in the expression of chemical structures used to deter herbivores should produce novel structures. Yet, just a small portion results in gene paralogs that can acquire potentially adaptive mutations under relaxed selection. These adaptive mutations eventually become fixed in the populations resulting in novel enzymatic functions. (*C*) Because the majority of gene duplications that result in novel defensive chemical structures are rare evolutionary events, chemical "key innovations" are conserved at deeper nodes of the phylogeny. (*D*) The second mechanism suggests that changes to the expression of individual or biosynthetically related metabolites result in the evolution of novel combinations of existing defense compounds leading to divergent chemical profiles among close relatives. (*E*) These changes might occur rapidly over evolutionary time leading to fixation on shallower nodes of the phylogeny. (*F*) The result is sympatric species that are highly divergent in their chemical profiles, as has been shown in the genus *Inga*.

zone. Several species within this clade have evolved more biologically derived compounds, including tyrosine and tyramine depsides, providing evidence for the "escalation of defense" through gradual modifications of core chemical structures. However, the mechanisms linking evolutionary changes driven by herbivores to reproductive isolation and subsequent speciation remain unclear. Marquis et al. (2016) proposed that coupled evolution of herbivore defense and pollinator attraction could act as a prezygotic isolation mechanism (Marquis et al. 2016; Maron et al. 2019) and that parapatric and allopatric speciation mediated by selection against hybrids and spatial variation in herbivores could trigger divergent selection along environmental gradients (Marquis et al. 2016). In yet another mechanism, recent research suggests hybridization may have played a significant role in the rapid diversification of sympatric *Inga* species (MJ Endara, unpubl.), providing genetic fuel for combinatorial speciation and reshuffling of existing genomic variation related to chemical defenses (Marques et al. 2019; Schley et al.

2020; Forrister et al. 2023). However, further theoretical and empirical work is required to integrate the evolution of chemical defenses with increased diversification in *Inga*.

Mutualistic Interactions

The diversification of the campanuloid clade in the bellflowers (family Campanulaceae) is one of the most striking examples of how ecological opportunity related to previously unoccupied habitats and unused resources triggers adaptive radiation in plants (Lagomarsino et al. 2014, 2016). In addition to orogeny and climate change, mutualistic relationships associated with seed dispersal and pollination syndromes contribute significantly to diversification rates in this clade (Lagomarsino et al. 2016). Bird-dispersed species with fleshy berries exhibit a 3.5-fold increase in diversification rates compared to species with abiotic dispersal (e.g., wind dispersal). A similar result arises when comparing species with vertebrate-pollinated flowers which exhibit an approximately sixfold increase in diversification rate relative to invertebrate-pollinated species (Lagomarsino et al. 2016). In the campanuloid clade, the increased speciation rates may be the result of floral isolation mediated by the interplay of floral morphology and pollinator behavior favoring the development of prezygotic reproductive isolation. In this case, the interplay between biotic and abiotic factors including floral morphology, pollinator behavior, and paleoelevation dynamics have contributed to the extreme diversification in these Andean bellflowers (Muchhala 2007; Lagomarsino et al. 2014, 2016).

Predator–Prey Relationships

Local adaptation in response to novel ecological conditions is not the only driver of adaptive radiation. Divergence in visual signals such as aposematic (warning) coloration has similarly produced a number of radiations in diverse animal taxa such as chemically defended butterflies (Kozak et al. 2015) and frogs (Symula et al. 2001) where differences in predation risk across geographic landscapes can drive phenotypic divergence. In the Neotropics, multiple radiations of mimicry rings can be found, perhaps best exemplified by *Heliconius* butterflies (Kozak et al. 2015; Merrill et al. 2015) and *Ranitomeya* poison frogs (Symula et al. 2001).

Heliconius butterflies appear to be much more complex than a simple radiation in warning colorations, as recent studies have revealed a much more intricate reticulated evolutionary history comprising multiple mimicry rings including members of various genera (Mallet and Gilbert 1995; Merrill et al. 2015). Diversification can be the outcome of a suite of different mechanisms, including host plant specialization (Merrill et al. 2013), predator avoidance (Langham 2004), and differences in visual sensitivities (Briscoe et al. 2010; Finkbeiner et al. 2014). Despite these adaptations and degree of specialization, highly reticulate evolutionary histories between divergent taxa have been documented (Mallet et al. 2007; Nadeau et al. 2012; Kronforst et al. 2013). As the greatest *Heliconius* diversity is found in contiguous regions of Amazonia, speciation rates do not seem to be entirely driven by diversification in allopatry. Evidence suggests that isolation and divergence with secondary contact and speciation among parapatric species is plausible in some instances (Mallet and Turner 1997; Rosser et al. 2014). However, diversification (or speciation) seems to have occurred at different pace within and between lineages in this group (Kozak et al. 2015).

Similarly, mimicry drove a well-studied adaptive radiation in the poison frog *Ranitomeya imitator*. This species is the mimic of four congeners throughout its geographic range. Across this distribution, genotypic and phenotypic variation between *R. imitator* and the other species diverges (Twomey et al. 2013). This pattern corresponds to radiations of mimetic phenotypes driven by divergent selection on color and pattern elements (Yeager et al. 2012). Geographic transitions between mimetic phenotypes result in narrow clinal transitions which are maintained by both natural and sexual selection (Chouteau and Angers 2012; Twomey et al. 2014, 2016). Divergent phenotypes are maintained for mimetic accuracy (Yeager et al. 2012; Twomey et al. 2013, 2014), such that predators

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recognize and avoid local phenotypes (Chouteau and Angers 2012).

Resource Uses and Ecological Release

Phyllostomid bats, known as Neotropical leaf-nosed bats, comprise remarkable ecomorphological diversity (Freeman 2000). Their extensive adaptations, including occupation of diverse dietary niches ranging from ancestral insectivory to carnivory, nectarivory, frugivory, and even dedicated sanguivory, make them an exemplary adaptive radiation (Martin and Richards 2019). South America hosts the greatest extant species diversity of phyllostomids, with diversification and disparification occurring together (Rojas et al. 2016). Notably, the fig-eating phyllostomid subfamily Stenodermatinae experienced a significant increase in diversification rates because of a reorganized skull architecture, enabling access to figs and entered a new dietary adaptive zone with lower trophic level and almost tripled diversification rates (Dumont et al. 2012; Shi and Rabosky 2015; Rojas et al. 2018). Other adaptive peaks are associated with omnivory, nectarivory, and highly advantageous short-faced skulls (Dumont et al. 2014). Recent analyses suggest that only some phyllostomid lineages capitalized on ancient preadaptations within the family or even the neotropical superfamily Noctilionoidea (Davies et al. 2020; Hall et al. 2021; Potter et al. 2021), which only some phyllostomid lineages capitalized on.

HYBRIDIZATION, INTROGRESSION, AND ADMIXTURE AS DRIVERS OF SPECIATION AND ADAPTIVE RESPONSE TO ECOLOGICAL OPPORTUNITY

Speciation, the formation of reproductive barriers among populations, can arise from divergent selection, such as ecological or sexual selection, or genetic incompatibilities due to genetic drift or genomic conflict (Seehausen et al. 2014). In addition, hybridization and polyploidization can also contribute to speciation (Feder et al. 2012). In particular, recent evidence suggests hybridization among closely related species can lead to extensive adaptive responses to divergent natural selection, challenging the necessity of reproductive isolation (Mayr 1947; Dobzhansky 1950; Seehausen et al. 2014; Grant and Grant 2019; Meier et al. 2019; Peñalba et al. 2024).

The arrival of a single lineage colonizer to a new habitat or ecological space where unused resources or no competitors (ecological opportunity) are present is a common scenario for an adaptive radiation (Schluter 2000; De-Kayne et al. 2024). In the presence of ample ecological opportunity, lineages radiate to occupy multiple vacant niches producing swarms of species with contrasting ecology. Multiple lines of evidence suggest that hybridization should trigger adaptive radiation in the presence of ecological opportunity (Meier et al. 2017, 2019; Meyer et al. 2017; Edelman et al. 2019). Whether hybridization predates adaptive radiation or closely related lineages arriving to a geographic area hybridize to successfully fill vacant niches is a matter of debate. Because hybridization of closely related lineages should not produce much genetic novelty and hybrids from distantly related lineages should be characterized by intrinsic incompatibilities (e.g., infertile, nonviable), one would expect that intermediate genetic distances between lineages maximize the role of hybridization in adaptive divergence (Meier et al. 2019).

Some lineages, like *Anolis* lizards, undergo rapid speciation and adaptive radiations, whereas others remain species-poor despite ecological opportunities (Losos and Thorpe 2004). The variance in speciation and adaptation rates is influenced by lineage-specific traits such as sexual selection, dispersal ability, phenotypic evolvability, and ecological versatility, all of which rely on standing genetic variation (Claramunt et al. 2012; Wagner et al. 2012; Rabosky et al. 2013; Stroud and Losos 2016; De-Kayne et al. 2024). High genetic variation facilitates speciation by increasing the potential for reproductive isolation and phenotypic evolution. It arises from new mutations or recombination of old genetic variants, forming genomic divergence islands resistant to gene flow (Han et al. 2017; Marques et al. 2019). Recent evidence also suggests that ancestral haplotypes act as genetic modules driving phenotypic diversity essential for species adaptation to changing environments (Rubin et al. 2022).

Recent genomic studies on neotropical fauna have started to untangle the genomic architecture of speciation and reproductive isolation during adaptive radiation. These studies have particularly highlighted the importance of the reassembly of old genetic variants into novel combinations for rapid speciation. For instance, genomic divergence islands should exhibit higher absolute differentiation (d_{XY}) relative to the genetic background in both sympatric and allopatric pairs of species. This has been found in recent studies of the genetic architecture of speciation and adaptation in Darwin's finches, suggesting that gene flow plays a minor role in the evolution of genomic divergence islands and supporting the hypothesis that haplotypes at genomic islands became genetically isolated before the rest of the genomes (Lamichhaney et al. 2015; Han et al. 2017). Further, adaptive introgression of ancient genetic variants at the *ALX1* and *HMGA2* genes underlying beak traits has played a key role in the adaptive radiation of Darwin's finches in the Galápagos islands (Han et al. 2017). Because beak morphology is associated not only with adaptation to food resources but also to species discrimination and mate choice, it is plausible that these loci are also involved in reproductive isolation. This has been corroborated in a study showing evidence for rapid hybrid speciation involving a founder male with standing genetic variation related to large and blunt beaks for the *HMGA2 L* and the *ALX1 B* alleles (Lamichhaney et al. 2015). Thus, ancient polymorphisms and hybridization via introgression may have facilitated the diversification of beak morphology in terms of ecological opportunity.

Similarly, introgression of the large-effect ancient allele *optix* in New World *Heliconius* butterflies has enabled rapid diversification and the generation of novel phenotypes (Reed et al. 2011). The evolution of novel wing scale patterns through hybridization represents the evolution of key innovations that facilitated the occupation of multiple different ecological spaces mediated by ecological opportunity. *Optix* is one of the major genes responsible for mimetic wing pattern evolution, controlling extreme red wing pattern variation in this rapidly radiating butterfly genus. The co-option of this pleiotropic gene contributed to the explosive diversification of wing patterns and adaptive radiation (Martin et al. 2014). Moreover, cross-species introgression of *optix* alleles is responsible for the evolution of multiple mimetic convergences across *Heliconius*. While introgression among *Heliconius* species is not directly involved in the formation of novel key traits, it is related to the propagation of adaptive variants across gene pools. In this way, hybrids may exhibit the effects of novelty through epistasis between wing pattern loci (Martin et al. 2014).

Speciation patterns in the Galápagos Islands endemic plant *Scalesia* are in agreement with an ancestral colonization in multiple islands followed by within-island speciation (Fernández-Mazuecos et al. 2020). In addition, signatures of hybridization in *Scalesia* radiation might be related to the evolution of partially heterogamous flowers via introgression (Lindhardt et al. 2009; Fernández-Mazuecos et al. 2020; Cerca et al. 2023). Strong signatures of hybridization during within-island speciation in *Scalesia* come from the evidence of introgression between four species with partially heterogamous capitula *S. retroflexa*, *S. incisa*, *S. hellerii*, *S. baurii*, and the widespread species with fully heterogamous capitula *S. affinis* (Fernández-Mazuecos et al. 2020). The occurrence of partially heterogamous capitula in *S. retroflexa* and *S. baurii* is the result of introgression with *S. affinis*. These introgression events are possible because the three species coexist in a single island in the Galápagos archipelago (Lindhardt et al. 2009; Fernández-Mazuecos et al. 2020).

Ecological opportunity related to novel trophic specialization is a key signature of the Caribbean pupfishes' adaptive radiation (Martin and Wainwright 2013; Martin 2016; McGirr and Martin 2017; Richards and Martin 2017). Accelerated rates of trophic diversification and shifts to new adaptive zones in *Cyprinodon* species are the product of fixation of de novo mutations during adaptive radiation toward distant phenotypic optima (Martin 2016; Martin et al. 2017; McGirr and Martin 2017). These adaptive peaks are related to the evolution of novel ecological traits allowing the occupation of new trophic niches in the specialist scale-eaters and snail-eaters compared to their single ancestral generalist species (Martin et al. 2017; McGirr and Martin 2017). Adaptive introgression of candidate genes associated with jaw development has been detected to be the result of selective sweeps favoring the speciation process of trophic specialists from a single ancestor from the Bahamas in the case of the *Cyprinodon* species in San Salvador (Richards and Martin 2017). However, speciation rates in San Salvador lineages are fivefold higher among populations within-island species compared to the role of adaptive introgression from Caribbean genetic diversity.

In sum, biased hybridization between some individuals from one species with heterospecifics should be related to adaptive introgression of ancient genetic variation from the donor species to a recipient species (Fig. 4). This process may fuel adaptive responses in the form of novel traits (key innovations) in response to new open

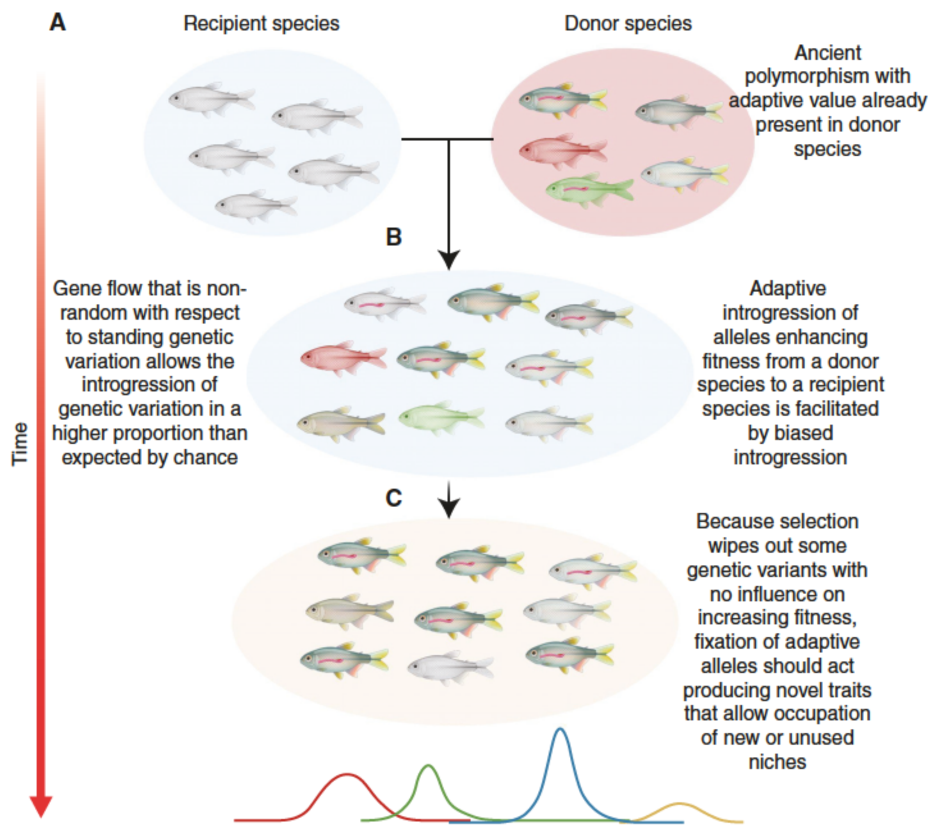

Figure 4. Hybridization determines which alleles initially move from one population to another. (*A*) Biased hybridization should facilitate nonrandom sampling of genetic variation to move from a donor to a recipient species. Because this genetic variation is the result of nonrandom hybridization with respect to segregating variation in a population there is an overrepresentation of genetic variation from donor species in the recipient species. If these variants are adaptive in the recipient species, such biases can enhance the likelihood of adaptive introgression. (*B*) Individuals carrying novel variants in the hybrid species are subject to selection in a similar ecological space to the recipient species (light blue background). (*C*) Over time these novel adaptive alleles are selectively favored if hybrids colonize a novel environment (light red background) or unused resources are available in such a way that hybrids descendants occupy these novel trophic niches. Deleterious variants (individuals in red and green color) are eventually lost. Colored waves represent niche partitioning among coexisting species in sympatry.

niches or unused resources (ecological opportunity). However, the prevalence of this process in producing adaptive radiation is still a matter of debate and needs to be further investigated.

FUTURE DIRECTIONS

The advent of metabolomics, genomics has opened the door to new questions and tests as some of the most recent studies in adaptive radiation have demonstrated. For instance, metabolomic analyses in the genus *Espeletia* showed that there is strong biogeographic differentiation in the secondary metabolites fingerprint of lineages distributed across the five main biogeographic regions in the paramos of Colombia and Venezuela (Padilla-González et al. 2017). These results support the hypothesis that diversification has resulted in sets of different groups of secondary metabolites, which might be responsible for widespread chemical innovations to deter different herbivores in the adaptive radiation of *Espeletia*. Further studies combining genomics and metabolomics in *Espeletia* and other systems might shed light on this finding. Identifying the set of genes responsible for the evolution of major secondary metabolites might enable us to detect differential selection in populations along spatial and environmental gradients, as has been found in hummingbirds.

Determining how genomic mechanisms facilitate or constrain adaptive radiation once a lineage encounters a new adaptive zone is a long-standing goal in evolutionary biology. Recent advances in genomic sequencing technologies have provided researchers with a powerful tool to study the genetic mechanisms underlying adaptation and speciation, as well as the timing and order of evolutionary events. For instance, when comparing two sympatric species, a positive relationship between speciation rates and the number of fixed indels relative to the time of their last most recent common ancestor (MRCA) should be a signature of divergent selection (McGee et al. 2020). This suggests that variation in speciation rates can be associated with whether a lineage has unusually many large indels for its age in ecologically associated genome regions (McGee et al. 2020). This highlights the need to analyze indels and single-nucleotide polymorphisms at the genome level in studies of adaptive radiation and speciation (McGee et al. 2020). Moreover, genomic data can provide valuable information about which indels are associated with ecological variables, capturing the major ecological dimensions of adaptive radiation. Combining genomically informed speciation research with macroevolutionary analyses of diversification enables discovering why some clades produce spectacular radiations, whereas others do not (Gillespie et al. 2020). Furthermore, genomic analyses can reveal how often repeated evolutionary transitions to new ecological niches are associated with the repeated genetic changes across independent lineages. In addition, genomics can provide insights into the molecular basis of morphological and physiological adaptations, and how genomic architecture and the source of genetic variation may promote or constrain adaptive radiation into a complex, multidimensional niche space (Marques et al. 2022).

Studying the adaptive landscape is crucial for understanding adaptive radiation as it provides insights into the evolutionary trajectories of species diversification. By examining how environmental factors impact the distribution of traits within a population, researchers can unravel the mechanisms driving adaptive radiations, shedding light on the origins and maintenance of biodiversity.

The adaptive landscape, originally defined by Wright (1932) as a multidimensional space in which each dimension corresponds to allele frequencies and mean fitness for a particular allele frequency to the height of this surface, has been fundamental to understanding how natural selection affects population survival and reproductive success. Simpson (1944, 1953) proposed a modification of this idea arguing that to better understand the role of divergent natural selection on survival and reproductive success in a particular environment we should account for phenotype differences in the adaptive landscape (Schluter 2000). Since then, the study of the adaptive landscapes has been focused on determining how morphological adaptation and ecological performance relate to ecological divergence (Grant and Grant 2002; Losos and Mahler 2010; Mahler et al. 2010; Brawand et al. 2014). Adaptive landscape topologies may represent the effects of stabilizing selection as a unimodal distribution in trait space, while disruptive selection should be related to multimodal distributions in trait space. When no selection is involved, the distribution should be uniform (Pfaender et al. 2016). Comparisons of variation-related fitness in a single phenotypic trait have proven effective in estimating the adaptive landscape for Darwin's finches (Schluter and Grant 1984; Lawson and Petren 2017). However, natural selection may affect multiple traits simultaneously and therefore adaptive landscapes could be used to analyze multivariate axes of phenotypic trait variation.

Studies performed in the neotropical cichlids, Neotropical leaf-nosed bats, and Darwin's finches have provided compelling evidence on how morphological divergence and ecological differentiation lead to differential fitness as reflected in adaptive peaks (Arbour and López-Fernández 2014; Lawson and Petren 2017; Beausoleil et al. 2023). Using Ornstein–Uhlenbeck models coupled with ancestral trait estimation and phylogenetic multidimensional analysis to define morphospace disparity, Arbour and López-Fernández (2014) detected seven adaptive peaks in the adaptive radiation of neotropical cichlids (Cichlinae). Three adaptive peak shifts were detected, related to the occupation of different regions of the biomechanics and feeding functional morphospace by different lineages, demonstrating functional disparity compatible with different selective regimes (Arbour and López-Fernández 2014). Likewise, Ornstein–Uhlenbeck analyses coupled with finite-element engineering models of the phyllostomid skull reveal four adaptive peaks associated with divergent diets, and corresponding functional performance within each adaptive zone (Dumont et al. 2014), with subsequent quantitative genetics and comparative analyses expanding the number of peaks while accounting for population variation (Rossoni et al. 2019). These examples demonstrate the power of trait comparative analyses to identify adaptive zones, and their links to functional performance in adaptive radiations.

Despite the availability of options for combining phylogenetics and genetics with phenotypic traits, there are few examples of adaptive landscapes in neotropical adaptive radiations (Beausoleil et al. 2023). However, novel technologies including genomics, proteomics, or metabolomics could enhance the analyses of adaptive landscapes or adaptive peak shifts. For instance, one could combine character displacement experiments related to pollinator access together with genomic and metabolomic analysis to shed light on the gene expression modules responsible for floral, ethological, and mechanical isolation in plant species coexisting in sympatry (Hodges and Derieg 2009; Moreira-Hernández and Muchhala 2019).

Trait utility and phenotype–environment correlations are key characteristics of adaptive radiations. Hence, to demonstrate the adaptive component of a particular radiation, it is necessary to test how well different phenotypes of descendant lineages fit into the divergent ecological spaces they occupy. Additionally, complementary evidence that confirms the differential performance of traits in contrasting environments is necessary.

BOX 2. OUTSTANDING QUESTIONS

1. How can adaptive introgression influence processes such as range expansion, exploring novel niches in response to global change, and avoiding extirpation/extinction?
2. What is the prevalence of adaptive hybridization in adaptive radiations?
3. How can we use genomic, metabolomic, and phylogenomic data in a standardized way in order to determine general patterns of ecology and evolution across systems in adaptive radiations?
4. How can we integrate geomorphological, environmental, and experimental data to fill gaps in our understanding of adaptive radiations?

Reciprocal transplant experiments in contrasting environments, physiological performance along environmental gradients, or experimental interspecific pollen transfer might be incorporated as sine qua nonanalyses for trait utility.

CONCLUDING REMARKS

The unique and complex geography of the neotropics, from its splendid isolation to the Andean uplift, is one of the main factors contributing to evolutionary radiations. Whereas many geological events have shaped the emergence of novel and complex habitats throughout South America, there is considerable variation in how different lineages have responded. Geomorphological dynamics of the Andean system, the Brazilian and Guiana Shield cratons as well as the historic events that shaped the Mata Atlantica are fundamental for the evolution of many iconic examples of adaptive radiation in South America, including among others *Espeletia*, bromeliads, primates, and *Heliconius* butterflies. Despite great advances, a better understanding of the processes underlying plant and animal adaptive radiations in the Neotropics requires integrating phylogenies with traits, traits with functional performance in particular niches, and, in some cases, traits to specific genes under natural selection (Box 2).

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