

EDITORIAL

Drivers of exceptional Neotropical biodiversity: an updated view

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The Neotropics, following the most common definition, comprise the tropical areas of the American continent from Mexico to Argentina (Morrone, 2017) and encompass the largest number of described species in the world, accounting for almost one third of global biodiversity (Raven *et al.*, 2020). This outstanding biodiversity fascinated early naturalists including Alexander Von Humboldt, who proposed the foundations of biogeography by observing the floristic gradients of the Andes (Humboldt & Bonpland, 1805), and Alfred Wallace, whose proposal of Amazonian rivers as isolation barriers for animals built one of the pillars of evolutionary theory (Wallace, 1852). The Neotropical region has also been an important natural laboratory for more recent advances in ecology and evolution, such as the role of the landscape and ecological interactions in the diversification of plants (Antonelli *et al.*, 2018; Rull & Carnaval, 2020).

Since the last special issue on the topic of Neotropical plant evolution (Hughes, Pennington & Antonelli, 2013), the field has seen increased advances in theory, data and methods, expanding our understanding of how such outstanding biodiversity was formed. These advances are allowing us to answer some remaining questions about what has driven the outstanding diversification of the Neotropical flora. In this special issue, we bring together 25 papers that,

in combination, use a multitude of approaches linking micro- and macroevolution to present a renewed view of the drivers of the exceptional biodiversity of the Neotropics. In particular, they emphasize the importance of geological and climatic changes throughout the Cenozoic in the diversification of the Neotropical flora. These studies also highlight the relevance of processes such as hybridization and polyploidization and the role of reproductive biology in generating floristic diversity. Moreover, it is widely recognized that biodiversity supports resilience and welfare of human societies. Neotropical ecosystems host extreme levels of biodiversity, but they are highly threatened by global environmental changes. The papers published in this special issue also offer an opportunity to reflect on how we can learn from the past to best plan for the future in the face of challenges that the region has been and is subject to such as biodiversity loss.

In a perspective article, Antonelli (2022) highlights not only the impressive levels of species diversity in the Neotropical region, but also the concerning disappearance of such richness. He contrasts the long-term evolution of Neotropical biodiversity with its recent and rapid decline due to anthropogenic factors. Although the Neotropics are the most biodiverse region in the world, currently 33% of all Neotropical species are threatened with extinction due to anthropogenic actions, such as intensification of land-use change (primarily driven by agriculture), direct

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exploitation, invasive species and climate change. In this perspective, the author also points out important opportunities for conservation and restoration of Neotropical ecosystems under the Post-2020 Global Biodiversity Framework actions to promote our peace with nature.

Geological information is crucial for understanding the deep-time origins and history of modern species diversification, but geological history from chronological and palaeoecological perspectives of many Neotropical domains, including the Amazonian region, are still under-studied and largely unknown (but see Hoorn *et al.*, 2010a, b; Latrubesse *et al.*, 2010). In a perspective paper in this issue, Hoorn *et al.* (2022) discuss the biogeographical importance of the Pebas system, a large wetland in western Amazonia, in generating biodiversity. The Pebas system is mainly thought to have promoted biota diversification because it is considered to have formed a biogeographical barrier for dispersal and gene flow for several terrestrial taxa, and it was a cradle of speciation for aquatic or semi-aquatic taxa. Hoorn *et al.* (2022), on the basis of the geological record of sediment deposition during the mid-Miocene, propose a new biogeographical model in which the Pebas system was a permeable system, promoting diversification in Amazonian biota by favouring biotic exchanges between diverse landscape dynamics. These findings suggest exchange and adaptation would have been common in the Pebas system and were also probably responsible for the astonishing species diversity in wetland systems in western Amazonia.

In the paper by Figueiredo *et al.* (2022), a phylogeny of Amazonian members of Marantaceae is used to propose a diversification model in which lineages with rapid growth strategies associated with fertile soils have faster rates of speciation. They show that the early diversification of rapidly growing lineages matches the timing of the origin of highly productive habitats in the Amazon after the uplift of the Andes in the Miocene. They suggest that this niche-trait relationship may have been key to the evolution of the high species richness in such tropical forests.

One of the most important events in the geomorphological history of the Cenozoic (from 65.5 Mya to the present) in the Neotropics was the uplift of the Andean Mountain chain caused by tectonic readjustments during the Palaeogene (Hoorn *et al.*, 2010a). In this special issue, three papers provide new insights into the contribution of the rise of the Andes to the evolution of observed biodiversity by altering the landscape of the Neotropics in several ways. Vieu *et al.* (2022) use a time-calibrated phylogenetic tree for *Macrocarpaea* (Griseb.) Gilg (Gentianaceae) to investigate the biogeography and diversification of the

humid mid-elevation montane forests of the Andes. They demonstrate that the uplift of the Andes provided an opportunity for continuous speciation by allopatry and that repeated founder events were important in the range expansion of the group. The authors also discuss the possibility that lineages of mid-elevation montane forests may be older and have diversified more slowly than those in the upper-elevation grasslands. Frankel, Murúa & Espíndola (2022) assemble plastomes for 14 species of *Calceolaria* L. (Calceolariaceae), an emblematic lineage of the Andes, and perform a phylogenomic analysis of the group. They provide a time-calibrated tree that resolves the backbone of the phylogeny of the genus. A biogeographical analysis shows that the two major clades in the group have colonized the whole geographical range of the genus through independent events. They also describe pollination strategies of the major lineages in the group and suggest further lines of research that will integrate these topics in the future. Similarly, Thode *et al.* (2022) reconstruct a time-calibrated phylogeny for *Sisyrinchium* L. (Iridaceae), using data from eight molecular markers. Their results show that the genus originated at higher elevations of the Andes in the Miocene, colonizing lowlands in the Neotropics afterwards. Higher extinction rates were correlated with higher elevations, and faster net diversification rates were correlated with lowland distribution.

Another important, but much less frequently discussed, orogenic event in the Cenozoic was the uplift of the Trans-Mexican Volcanic Belt. Romero-Soler *et al.* (2022) use a phylogeographic and population genetics approach to trace the evolutionary history of the species of *Bakerantha* L.B.Sm. (Bromeliaceae), a dioecious and narrow endemic group sometimes included in *Hechtia* Klotzsch. This study shows that speciation in this genus began in the late Pliocene and the rise of the Trans-Mexican Volcanic Belt promoted a barrier that isolated populations of *Bakerantha* spp. to its north and south, resulting in speciation by vicariance.

Although more stable, the landscape formation of the eastern side of South America also provided an ideal arena for important events of diversification in the Cenozoic. For instance, Bacci *et al.* (2022) provide a time-calibrated phylogenetic tree and historical biogeographical analysis of *Bertolonia* Raddi (Melastomataceae), a group endemic to the Atlantic Forest. They show that the diversification of the group dates back to the Oligocene. Furthermore, the two major clades in the genus are almost entirely endemic to northern and southern portions of the Atlantic Forest, respectively, indicating that historical barriers promoting evolutionary divergence in this biota may be older than previously expected. Larocca *et al.* (2022)

demonstrate that the timing of marked disparification (trait evolution) and species diversification are uncoupled in Velloziaceae from rocky outcrops of the campo rupestres, a biota associated with ancient mountains in Brazil. The authors find a signal for an early burst in diversity of life forms in the mature radiation of *Vellozia* Vand. and a still-accelerating rate of disparification in the more recent radiation of *Barbacenia* Vand.

It is widely argued that microevolutionary mechanisms are crucial drivers of species diversification. In fact, population differentiation is a first key step in diversification, implying that population differentiation and species diversification should be associated over deep evolutionary time (Harvey *et al.*, 2017). From this point of view, it is essential to establish a link between microevolutionary mechanisms (gene flow, genetic drift, mutation and natural selection) and macroevolutionary patterns (speciation and extinction). This connection, although challenging, is likely to provide important answers to the open questions about the diversification dynamics of the Neotropical biota. One example of linking both diversification scales is presented by Souza Neto *et al.* (2022) in a review of macro- and microevolution in Myrteae, the most species-rich tribe of Myrtaceae. The authors provide the first overview of evolution and diversification studies on Neotropical Myrteae, unravelling important progress in recent years. Phylogenetic analyses and identification of new morphological traits have contributed to the systematic and evolutionary understanding of Myrteae. Although the microevolutionary studies (population genetics and phylogeography) in Myrteae are still limited, this review reveals significant microevolutionary mechanisms influencing lineage diversification in some species of Myrteae.

From a population-level perspective, André *et al.* (2022) examine genetic structure and phylogeographic patterns of the understory *Chamaecostus subsessilis* (Nees & Mart.) C.D. Specht & D.W. Stev. species complex from South American seasonally dry forests, a phytogeographic domain that is mainly composed of savannas and dry forest patches across the Cerrado and southern Amazon. Their results, based on a large dataset of genomic sequences obtained from targeted capture sequencing, reveal deep phylogenetic structures (15–30 Mya) separating populations by the Tocantins River and lack of gene flow between Amazonia and Cerrado biomes. Such spatial arrangements among Amazonian and Cerrado lineages of the *C. subsessilis* complex suggest that their microevolutionary drivers are possibly linked to environmental gradients. Similarly, Franco *et al.* (2022) study the genetic diversity of the insular endemic species of cactus (*Cereus insularis* Hemsl.) from

Fernando de Noronha Islands (FNI) and its genetic relationship with the mainland *C. fernambucensis* Lem. The authors find similar patterns of genetic diversity in the insular and mainland populations, but compared with microendemic cactus species (Solórzano *et al.*, 2009; Khan *et al.*, 2018) the genetic diversity of both species is low. Recurrent gene flow among populations of *C. insularis* with mainland populations after the colonization of FNI have contributed to the maintenance of genetic diversity in the *C. insularis* lineage, suggesting that the hypothesis of genetic diversity erosion in *C. insularis* due to long-standing genetic drift could be rejected.

Population-level studies in this special issue also highlight the importance of climatic oscillation during the Pleistocene in promoting origin and diversification in several Neotropical plant species complexes. In a perspective article, Freitas (2022) reviews processes that drove diversification in *Petunia* Juss. (Solanaceae) by compiling data from studies describing genetic and morphological diversity for this and other Neotropical genera. This review indicates that migration during the Quaternary period seems to explain the genetic variability in *Petunia* and other herbaceous genera in South America. Inter- and intraspecific comparisons in *Petunia* reveal several examples supporting the idea that the centre-periphery hypothesis drove the genetic, morphological and even mating system diversity in this genus. A similar pattern has also been observed for plant species from different biomes in the Neotropical region (Thode *et al.*, 2014; Teixeira *et al.*, 2016; Mäder *et al.*, 2021). Souza *et al.* (2022) analyse the genetic diversity, population structure and gene flow in three rare and endemic species from subtropical highland grasslands in southern South America (*Petunia bonjardinensis* T. Ando & Hashim., *P. reitzii* L.B. Sm. & Downs and *P. saxicola* L.B. Sm. & Downs) and do not find genetic evidence of bottlenecks, suggesting that rarity is probably historical for these species. As expected, the species with the largest occurrence area and population sizes (*P. bonjardinensis*) has higher genetic diversity than the more restricted species. Genetic diversity levels were also influenced by reproductive biology and recent habitat loss, whereas the landscape influences the genetic structure, historical migration and founder effects. The authors also discuss the role of Pleistocene climate cycles as an important factor explaining species genetic diversity. On the basis of the fact that these species are endangered, the authors recommend urgent actions to preserve these species *in situ* and *ex situ*.

Climatic oscillations during the Pleistocene are also linked to historical connections between the Amazonian and Atlantic Rainforest floras, as investigated by Pessoa *et al.* (2022a). These authors analyse the phylogenetic relationships and biogeography of the *Epidendrum*

latilabre Lindl. (Orchidaceae) species complex, finding that climatic shifts during the Pleistocene were probably an important driver of speciation events in the species complex. Moreover, their results indicate that the south-east/north-west bridge and northern/north-eastern coastal route were possibly occupied by the ancestor of *E. latilabre*, whereas the alternative route across the South America Dry Diagonal was highly improbable.

A population-level study by [Teixeira et al. \(2022\)](#) on *Nicotiana forgetiana* Sander ex W. Watson and *N. alata* Link & Otto (Solanaceae) reveals floral morphology variation across the geographical distribution of the species in southern Brazil, an area marked by a mosaic of open grasslands and *Araucaria* Juss. Forest and by high plant endemism. The authors apply geometric morphometric analyses and ecological niche modelling to shed light on the patterns underlying intraspecific floral shape variation. They observe that the floral shape variation is related to abiotic gradients, such as temperature, precipitation and elevation. They also suggest that climate oscillations during the Pleistocene may have influenced the population dynamics in *N. alata* and *N. forgetiana* and their pollinators. [Solís-Neffa et al., \(2022\)](#) perform current and past niche modelling, combined with intraspecific genetic and cytogeographic variation, to show that the *Turnera sidoides* L. autopolyploid complex (Passifloraceae) has evolved through allopatric speciation since early Pleistocene. They also present results on diversification of this species complex in the Neotropical Chachean domain due to independent polyploidy series in each morphological lineage, in which different cytotype series are reproductively isolated and have contrasting ecological requirements.

Also at the population level, [Vicente-Silva et al. \(2022\)](#) investigate the hypothesis that genetic isolation exists among populations of *Deuterocohnia meiziana* Kuntze ex Mez (Bromeliaceae) on rock outcrops in Brazil. They demonstrate that only populations separated by > 70 km show genetic differentiation, adding to our understanding of connectivity and isolation of naturally fragmented populations and highlighting the role of biotic and abiotic drivers for genetic differentiation.

Although hybridization is widely recognized as an important driver of diversification and extinction, its role in the diversification of the megadiverse Neotropical flora is still largely under-studied. In their review in this special issue, [Schley, Twyford & Pennington \(2022\)](#) assess 60 studies of hybridization in Neotropical plants and discuss several outcomes of hybridization ranging from short-term effects, including increased ecological amplitude with transgressive hybrid phenotypes and genetic swamping, to long-term outcomes, such as generation

of new species and rapid diversification of species-rich radiations, especially in the Andean flora.

Ancient hybridization events are revealed by [Pessoa et al. \(2022b\)](#), who hypothesize that past hybridization/introgression events were involved in creation of substantial chromosome number variation in several species of *Epidendrum* L. (Orchidaceae) independent of polyploidy. They demonstrate that major karyotype changes happened after species divergence in nearly all cases and many ancestral karyotypes were unchanged. Moreover, chromosome gains, polyploidy and decreasing dysploidy were the most frequent changes estimated for these species.

[Jantzen et al. \(2022\)](#) also use a phylogenomic approach to reconstruct the evolutionary history of *Tibouchina* Aubl. s.s. (Melastomataceae), a lineage particularly diverse in the Cerrado, the savannas of central South America. Their analyses recover evidence of events of polyploidization and hybridization and ecological divergence as important drivers in the evolution of the group. They also emphasize that many of the species-rich Neotropical groups that remain under-studied may be even larger than previously thought, as demonstrated by the polyphyly of species in *Tibouchina* s.s.

Reproductive biology as a whole, including shifts in pollination, also remains under-studied in the Neotropics and may provide good model systems to link micro- and macroevolution. From a microevolutionary perspective, [Turchetto et al. \(2022\)](#) evaluate the mating system and gene flow impact on genetic diversity and population structure in *Petunia exserta* Stehm. (Solanaceae), an endemic species to small shelters in rocky towers in the Pampa grassland. The authors report low genetic diversity and a homozygous excess in *P. exserta* compared with its congeners and a strong genetic structure and that the species has a mixed mating system with high selfing rates. It has been shown that self-compatibility allowed *P. exserta* populations to colonize new habitats. These divergences may be reflected in morphological divergences across longer time scales. For instance, [Kriebel et al. \(2022\)](#) analyse the evolution of stigma shape in c. 400 species of *Salvia* L. (Lamiaceae). They make use of several phylogenetic comparative methods to demonstrate that a set of stigmatic traits, including longer upper stigma lobe and presence of a stigmatic brush, evolve in a correlated fashion and are linked to hummingbird pollination in the group. Finally, they show that these traits are still observed in many extant species of the group, despite repeated shifts back to bee pollination.

Understanding biodiversity from a community perspective is also crucial to reveal the processes responsible for the Neotropical hyperdiversity. Biotas are formed by interactions between taxa

that coexist in a given ecosystem. In this respect, areas of endemism allow the identification of these sets of taxa and the characterization of biogeographic regions, and their description is an important step in planning future conservation policies. In this special issue, [Dornelles *et al.* \(2022\)](#) and [Narváez-Gómez *et al.* \(2022\)](#) analyse areas of endemism at different spatial scales. [Dornelles *et al.* \(2022\)](#) analyse areas of endemism for the flora of the *Araucaria* Forest. Their analyses pinpoint the areas of greatest endemism in the forests as the southern plateau between the states of Rio Grande do Sul and Santa Catarina. [Narváez-Gómez *et al.* \(2022\)](#) analyse endemic areas across the Neotropics using a large data set of distribution with > 20 000 unique locality records of species belonging to tribe Bignonieae (Bignoniaceae). The results identify 70 areas of endemism across three spatial scales in the Neotropics. In general, their findings suggest that areas of endemism in Bignonieae are congruent with those previously described for other groups of plants and animals in the Neotropics.

To conclude, the papers in this special issue help us take further steps in answering the long-standing question of why the Neotropics are the most biodiverse region in the world. This question, asked by naturalists and botanists over the last two centuries, has remained unanswered until recent studies started to shed light on the drivers of the outstanding Neotropical biodiversity. The continuing accumulation of biological data, especially from poorly known plant groups and under-collected areas, and integration of different research fields are still required to fully understand the drivers behind the exceptionally rich Neotropical flora.

This special issue also contributes to the aim of achieving diversity, equity and inclusion of unrepresented research teams in botany and evolutionary biology by bringing 20 papers (out of 25) led (first or senior author) by Latin American researchers. We are also happy to see that 14 out of 25 papers have been published by women as the first or senior author, and we hope that this issue will contribute to the aim of inspiring equity, diversity and inclusion in science. Finally, we express our gratitude to many referees who kindly donated their time and work to the improvement of the papers published in this special issue.

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