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Thematic Review

A multidisciplinary framework for biodiversity prediction in the Brazilian Atlantic Forest hotspot

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Abstract: We briefly describe selected results from our thematic project focused on the biodiversity of the Atlantic Forest (“AF BIOTA”), which was jointly funded by FAPESP’s BIOTA Program, the U.S. National Science Foundation Dimensions of Biodiversity Program, and the National Aeronautics and Space Administration (NASA). As one of the five most important hotspots of biodiversity in the world, the Atlantic Forest (AF) holds less than 16% of its vegetation cover, yet, amongst the hotspots, it still harbors one of the highest numbers of species, including endemics. By gathering specialists across multiple disciplines (biology, geology, engineering), we aimed to understand how this megabiodiversity was built through time, informing biodiversity science and conservation. Among the results, we trained 18 Master’s and 26 Ph.D. students, published more than 400 peer-reviewed papers that improved our knowledge about the forest’s biologic and climatic diversity and dynamics through time, developed new analytical methods, produced outreach videos and articles, and provided data to help define biodiversity conservation policies.
Keywords: *Biogeography; Phylogeography; Paleoclimate; Paleovegetation; Geogenomics.*

Integrando disciplinas para a predição da biodiversidade da Floresta Atlântica no Brasil

Resumo: Descrevemos de forma resumida resultados selecionados do nosso projeto temático com foco na biodiversidade da Floresta Atlântica (“AF BIOTA”), que foi financiado pelo BIOTA FAPESP e pelo programa “Dimensions of Biodiversity” da “U.S. National Science Foundation” e “National Aeronautics and Space Administration” (NASA). Devido à sua megabiodiversidade (que inclui várias espécies endêmicas), e por restar menos de 16% da vegetação original, a Floresta Atlântica (FA) é uma das cinco áreas mais importantes para a biodiversidade do planeta (“biodiversity hotspot”). Reunimos especialistas de diversas disciplinas (biologia, geologia, engenharia) visando compreender como essa megabiodiversidade evoluiu ao longo do tempo e fornecer informações científicas para a sua conservação. Dentre os resultados obtidos, nós formamos 18 mestres e 26 doutores, publicamos mais de 400 artigos científicos que aumentaram o conhecimento sobre a diversidade biológica e climática da FA e sua dinâmica ao longo do tempo, desenvolvemos novos métodos analíticos, produzimos material de divulgação científica e fornecemos dados para desenvolver políticas públicas de conservação da biodiversidade.
Palavras-chave: *Biogeografia; Filogeografia; Paleoclima; Paleovegetação; Geogenômica.*

Introduction

1. Context

The Atlantic Forest (AF) is one of the top five hotspots of biodiversity on the planet (Myers *et al*. 2000). It houses high numbers of species of plants and animals (e.g. 20,000 out of 300,000 plants on Earth, and 1,361 out of 27,298 of our planet's vertebrate species, Myers *et al*. 2000), including various endemic species (2.7% of the world's plants and 2.1% of total vertebrates exclusively occur in the AF, Myers *et al*. 2000). This is in spite of the high levels of degradation imposed to this region; less than 16% of this domain remains forested today (Ribeiro *et al*. 2009). Given the importance of the AF, several of us have been focusing our studies on AF organisms since the early 2000s - if not before. FAPESP has funded several of those research projects (Thematic grants: 98/10018-2, 99/05446-8, 03/14106-3; PIPE grant 10/51390-5; Young Researcher grants: 06/06761-0, 12/17517-3; Regular grants: 00/05729-9, 07/52906-2, 07/54498-9, 08/06604-7, 09/12989-1, 10/20560-2, 11/50394-0, 12/02969-6, 16/00299-4), which aimed to describe the forest's biodiversity (including taxonomic and biogeographic analyses) and paleoclimate. In 2013, we were awarded a thematic BIOTA grant jointly funded with the U.S. National Science Foundation (NSF) and the National Aeronautics and Space Administration (NASA) that aimed to apply a multidisciplinary framework to explain and help preserve its biodiversity patterns. We nicknamed our project "AF BIOTA". Here we describe how our project was designed, our main questions, and results. We also discuss how those results have been used to help conserve the biodiversity of this fascinating system, and address future perspectives.

2. Design and coordination

In November 2011, FAPESP and NSF co-organized a meeting in Atlanta to discuss strategies and build collaborations that could be jointly funded by the two agencies, under the umbrella of a new program, Dimensions of Biodiversity. Two years later, we submitted a proposal to that joint call and we were given an award. The US team was coordinated by PI Carnaval and Co-PI Michelangeli, and the Brazilian team was coordinated by PI Miyaki. Our AF BIOTA project gathered, for the first time, various members of our research team to develop mechanistic predictions of biodiversity patterns in the AF to help guide conservation and research. Together, we linked spatial patterns of biodiversity with their underlying ecological mechanisms and historical climatic and demographic processes. We integrated data from various disciplines (evolution, population genetics and genomics, physiology, geography, paleoclimatology, paleovegetation, taxonomy, and remote sensing) to describe and explain spatial patterns of lineage and species-level diversity, endemism, and turnover. It has been a rewarding challenge to combine data and ideas from biologists, geologists, and engineers, and, with time, new members joined us. As a group, we have reconstructed population histories across co-distributed taxa to infer community-level macro-ecological processes of community assembly, allowing us to detect forces behind regional biodiversity patterns, and to understand how changes in the environment differentially affected species distributions. Initially, our genetic data were mostly based on sequences of a few nuclear loci and mitochondrial or chloroplast genes (Cabanne *et al*. 2014, Carnaval *et al*. 2014, Dantas *et al*. 2014). However, the award allowed us to progressively generate new or leverage ongoing next-generation sequencing (NGS) efforts for use in phylogenomics and phylogeographic studies of AF taxa (Aguirre-Santoro *et al.* 2016, Amaral *et al*. 2021, Goldenberg *et al*. 2018, Reginato & Michelangeli 2016, Prates *et al*. 2016b, Thom *et al*. 2021). Those reconstructions of population histories have helped us to identify and prioritize regions of heightened stability and genetic diversity, identify areas of connectivity, and help determine areas and groups under greater extinction threats.

Our pre-award studies sought to understand the spatio-temporal pattern of distribution of the genetic variability of a selected AF species (e.g. reptiles: Pellegrino *et al*. 2005; birds: Cabanne *et al*. 2007, 2008; amphibians: Carnaval *et al*. 2009), detecting evolutionary differentiation of lineages that occurred in the south and in the north of the AF. Thanks to the BIOTA/Dimensions of Biodiversity award, we were able to combine and reconcile these and other published data and summarize patterns of genetic diversity along the forest - building from information about the fauna and flora (Cabanne *et al.* 2016, Carnaval *et al*. 2014, Peres *et al*. 2020) and harmonizing data across labs and research groups (Brown *et al.* 2020, Paz *et al.* 2020, 2021). To interpret those patterns, we employed newly generated data on the paleoclimate of the AF. Also back in 2013, members of our team published an analysis of oxygen isotope ratios in calcium carbonate cave formations (speleothems) to describe an anti-phased paleo-precipitation pattern in South America during the last glacial-interglacial periods (Cheng *et al*. 2013). For instance, the climate during the Last Glacial Maximum (LGM, circa 20 thousand years ago, kya) to the early-mid Holocene (circa 5-10 kya) in the southern AF shifted from relatively wet to moderately dry conditions, while the northern AF shifted from severely dry to substantial wet conditions. Those insights helped us to build our project's framework that recognized the heterogeneous environments and a complex evolutionary history of the AF along its broad latitudinal and altitudinal gradients.

Main Results

1. Academic

Since the inception of AF BIOTA, 18 students defended their Master's Thesis and 26 students received their Ph.D. degrees while working on topics directly tied to the project - both in Brazil and the United States. We also trained 15+ undergraduate students and 18 postdocs, many of whom now hold tenure-track faculty positions. Before the COVID-19 pandemic, we hosted annual project meetings in São Paulo (2014: 4 days, 70+ participants; 2015: 4 days, 50+ participants; 2016: 2 days, 25+ participants; 2017: 1 day, 5 participants; 2018: 5 days, 30 participants, including a 3-day training workshop on Genomic Data Processing in Ecology and Evolution to Brazilian graduate students; 2019: 2 days, 20+ participants). Several of those meetings counted with the presence of invited speakers or new collaborators who helped us design and execute part of our strategic research plan. Leveraging the annual meetings, we hosted two symposia at FAPESP (2014: 10 talks and 15 posters, 260+ participants; 2019: 13 talks, 90+ participants), where we presented our findings to the general and scientific public. The training workshop on Genomic Data Processing in Ecology and Evolution, organized by two of our former postdocs in 2018, is freely available online (https://radcamp.github.io/ and https://radcamp.github.io/AF-Biota/).

As a result of our collaborative work, various of our team members visited project collaborators, +19 students were exchanged between Brazilian and US research groups - especially between USP and the City College of New York, but also involving UNESP, Universidade Federal do Paraná, and the New York Botanical Garden. Our international team worked together in various field trips to collect biological samples (invertebrates, vertebrates, plants), geological samples (paleopolen, speleothems), and environmental data (humidity, temperature, precipitation).

Below we describe some selected results produced by our team:

1. Our project improved documentation of the AF diversity. Some examples include the description of one new family of harvestmen, four tribes of Melastomataceae, and 85 new species of animals or plants (four onychophorans, 22 arachnids, 17 butterflies, two lizards, one treefrog, seven Bignoniaceae, two Eriocaulaceae, one Myrtaceae, four Cyperaceae, and 27 Melastomataceae; Supplementary Material S1). To improve our understanding of their evolutionary relationships, we contributed with 31 phylogeographic studies (12 of birds, seven of arachnids, two of bees, seven of amphibians/reptiles, one of butterflies, and two of plants; Supplementary Material S2) and 95 phylogenetic studies with at least one AF taxon (12 of arachnids, one of velvet worm (onychophora), 22 of butterflies, five of birds, 27 of amphibians or reptiles, one of mammal, two of fish, and 25 of plants; Supplementary Material S3).

2. Several new analytical methods that process genetic and genomic data, specially focusing on multi-taxon tests, were developed by the research group of US Co-PI Hickerson. One of these methods detects concerted demographic histories across an ecological assemblage accommodating dataset heterogeneity (such as variability in effective population size, mutation rates, and sample sizes across species), and exploits the statistical strength from the simultaneous analysis of multiple species (Chan *et al*. 2014). This can increase our understanding of the impact of historical climate change by determining what proportion of the community responded in concert or independently, and can be used with a wide variety of comparative phylogeographic data sets. Also, it helps to understand the effects of future climate and landscape changes and the resulting acceleration of extinctions, biological invasions, and potential surges in adaptive evolution. Another method developed by our group is the use of the aggregate joint site frequency spectrum (ajSFS) to compare divergences across multiple sister population pairs (Xue & Hickerson, 2020). These methods were successfully tested on real datasets and revealed complex and flexible co-demographic patterns.

3. A 14 m deep sediment core retrieved in 2014 from the Colônia crater, south of the city of São Paulo, recorded the local past vegetation dynamics. Led by collaborator Ledru, the chronostratigraphic analysis of the core revealed that it spans the last 1.5 million years and that the Colônia basin formed between 11.2-5.3 million years ago (Simon *et al*. 2020). Data from the top portion of the core (180,000 years ago [180 ka] until the present) indicated that: 1) a cool mixed evergreen forest was present in the region between 180 and 45 ka, being replaced by rainforest, 2) the temperature around 57-29 ka (penultimate glacial period) was cooler than during the Last Glacial Maximum (23-29 ka), and 3) wet summer season became longer from 95 ka until the present (Rodríguez-Zorro *et al*. 2020). These results show that tropical forest dynamics display different patterns than mid-latitude areas during the last 180 ka, and demonstrate the importance of paleoecological data to help draw a more detailed scenario of the AF vegetation dynamics through time.

4. Geochemical analyses of various speleothems from South America helped to reconstruct its past rainfall pattern. The research group of the Brazilian Co-PI Cruz analyzed a stalagmite from a cave in the state of Santa Catarina, southeastern Brazil, that recorded multidecadal to centennial changes in precipitation during the Holocene. The comparison of the precipitation dynamics with those in other speleothems revealed that the amount of rainfall in northeastern and southeastern Brazil was markedly anti-phased and was possibly mediated by solar irradiance (Bernal *et al*. 2016). Two other speleothems from the Peruvian Amazon also provided records on high-resolution paleo-precipitation changes (Bustamante *et al*. 2016). These latter records are very relevant to understand the climate fluctuations that occurred in southern Brazil because this region is highly impacted by moisture availability and deep convection over the Amazon region (Novello *et al*., 2019). In addition, we have linked changes in Amazon climate to precipitation variability on the eastern coast of Brazil and the Andes Cordillera (Strikis *et al*. 2015; 2018). The establishment of long-term paleo-precipitation patterns is of great relevance for discussing possible vegetation connections among forest biomes - such as AF and Amazon. These connections are a key factor for the dispersal of species and biogeography features. Pollen studies revealed that the dispersion of montane forest species from the north to the south of the AF are linked to some wet events reconstructed in these studies based on speleothem isotope records (Pinaya *et al*. 2019).

5. Information on the physiological thresholds of the local fauna and flora is important given expected scenarios of future climate change, especially higher global temperatures. Thus, our herpetology group analyzed thermal thresholds in lizards of the AF. One such investigation described how thermal tolerance can be measured in lizards using panting behavior, mass loss, and locomotion loss (Camacho *et al*. 2018). Another paper discussed how biotic interactions may play an important role, along with thermophysiological constraints, in limiting the altitudinal range of montane lizards (Strangas *et al*. 2019).

6. An analysis of a floristic database of 2,616 species of trees from the central region of the AF, combined with geo-climatic data, revealed that tree species composition shows pronounced turnover north of the Rio Doce, where both humidity and energy levels shift. The study showed that climatic conditions, rather than the river itself, influence biogeographical shifts of the AF flora (Saiter *et al*. 2016). Shifts in community composition near the Rio Doce had been previously observed by our team when analyzing genetic diversity patterns of 25 vertebrates (Carnaval *et al*. 2014). A similar turnover near the Rio Doce was also observed in an AF database of (ca. 600) harvestmen species (Nogueira *et al* 2019a, 2019b). Phylogeographic patterns observed in a harvestmen species nonetheless detected genetic breaks that are parallel to the coast; this low mobility organism revealed new spatial patterns, with much older divergences than those revealed by other groups of animals (Bragagnolo *et al*. 2015, Peres *et al*. 2017, Castro-Pereira *et al*. 2021). Our work has revealed both shared and unique patterns of geographic distribution of genetically differentiated lineages, and also detected varying levels of divergence across co-distributed lineages (see review by Peres *et al*. 2020).

7. We integrated data from hundreds of plant species (melastomes and bromeliads), vertebrates (amphibians, reptiles, birds), and invertebrates (butterflies) across our research groups to map patterns of taxonomic and phylogenetic diversity, endemism and turnover along the AF based on verified phylogenetic, phylogeographic, taxonomic, and locality data.

The results highlighted the importance of conserving the remaining forest cover of the AF, especially along the Serra do Mar, which holds a relevant portion of the AF biodiversity (Brown *et al*. 2020). Using an extended dataset, we analyzed if environmental conditions predict the distribution of these multiple groups of organisms in the AF, despite their ecological differences. The results showed that current precipitation, and precipitation stability over the past 120 kyrs, are strongly correlated with species richness and phylogenetic diversity. However, our results are less homogenous across groups when phylogenetic endemism is considered (Paz *et al*. 2020, 2021).

8. Our studies also revealed that the history of the AF is deeply connected with other Neotropical biomes, such as the Amazon forest (lizards: Prates *et al*. 2016a, b; paleoclimate: Novello *et al*. 2017, 2019) and the Andean forest (birds: Trujillo-Arias *et al*. 2018, 2020; lizards: Prates *et al*. 2017; plants: Meyer *et al*. 2021). For instance, the spatial distributions of genetic lineages of three lizard species suggest that ancestral Amazonian populations synchronously colonized the AF, and, for a well-sampled species, genomic data indicate that an eastern Amazonia ancestral population colonized the AF (Prates *et al*. 2016a, b). A study of speleothems from a cave in the state of Mato Grosso do Sul (city of Bonito), when compared to other records in South America, revealed that the LGM was wetter than the early- and mid-Holocene and produced a precipitation (monsoon) belt from the Andes to southeastern Brazil (Novello *et al*. 2017, 2019). This finding is congruent with paleovegetation reconstructions that suggest that forests expanded in southern and central Amazonia in this period. Moreover, two phylogeographic studies of bird species tested whether past connections between the AF and the humid Andean forest occurred through the Cerrado (savannah-like biome in the South American open vegetation diagonal) or the Chaco (further south). The results indicated that connections were recurrent and that were more probable through the Cerrado and/or at the transition of Cerrado and Chaco (Trujillo-Arias *et al*. 2018, 2020). In another study focused on two montane lizard species, our phylogenetic results indicated colonization of the AF from western South America (Andes and Guiana shield) through the intervening lowlands (Prates *et al*. 2017).

9. In spite of the fact that the Atlantic Forest has been relatively well sampled compared to other Neotropical biomes, we also showed that certain areas are in much need of further exploration, particularly northern Espírito Santo and southern Bahia (Bacci *et al*. 2018). This is particularly important as this area presents high levels of endemism, and species turnover for both plants and animals (e.g. Carnaval *et al*. 2014; Nogueira *et al.* 2019a, 2019b; Reginato & Michelangeli 2020; Bacci *et al*. 2021).

The collaborative nature of the AF BIOTA project enabled several high impact publications. Among other journals, our findings have been published in **Scientific Reports** (Azevedo *et al*. 2019, De-Silva *et al*. 2017, Novello *et al*. 2016, 2017, Pinaya *et al*. 2019, Rodríguez-Zorro *et al*. 2020, Utida *et al*. 2019), **Nature Communications** (Deininger *et al*. 2020, Thom *et al*. 2021), **Science Advance**s (Rozendaal *et al*. 2019, Thom *et al*. 2020), **Nature Ecology and Evolution** (Poorter *et al*., 2019), **Proceedings of the National Academy of Science of the United States of America** (Cheng *et al*. 2020, Prates *et al*. 2016 b, Stríkis *et al*. 2018), **Proceedings of the Royal Society of London** (Carnaval *et al*. 2014), and **Evolution** (Amaral *et al*. 2021, Xue & Hickerson 2020).

Collectively, the AF BIOTA team published more than 400 peer-reviewed papers, contributed with 11 book chapters, and edited one book. We highlight the publication in 2021 of a special issue of the journal **Molecular Phylogenetics and Evolution** showcasing the evolution of the AF in 17 papers. Collaborators Amaral and Cabanne, US Co-PI Michelangeli, and Brazilian PI Miyaki edited this special issue. US PI Carnaval also co-edited a book on the topic of Neotropical Diversification (Rull and Carnaval, 2020). These results were also presented in scientific meetings as numerous seminars, plenary talks, posters, and oral presentations.

2. *Unfolding*

AF BIOTA has also impacted biodiversity scientists more broadly. Given the high number of engaged female students in the research group of the US PI A. Carnaval, a Women in Science group was funded at the City College of New York (CCNY WinS; http://ccnywins.wix.com/womeninscience), inspiring other students and postdocs in Brazil. CCNY WinS increases awareness about the status of Women in Science within the CCNY community (undergraduate and graduate students, postdocs, staff, early career and tenured faculty members) through meetings, training workshops, social gatherings, a peer mentoring program, and seminars. Carnaval has been engaged in empowering Latin-American women and early career biodiversity scientists and, along with students and collaborators, co-authored a paper published on the topic in **Science** (Bernal *et al*. 2019). Moreover, inspired by a talk by US PI Carnaval on the multidisciplinary aspects of AF BIOTA, the City College Science Division received a $1,000,000 donation to jumpstart the creation of a multidisciplinary Center for the Study of Biodiversity and Environmental Change. The Center's main aim will be to support biodiversity research by CCNY's students – through seed and travel grants and training. Given the large number of underrepresented minorities and economically under-served students at CCNY, this can have broader impacts in New York and beyond.

3. *Outreach*

As part of its outreach mission, the AF BIOTA team also worked on multiple science communication projects, sharing findings with the general public through interviews, written notes, videos, and an exhibit at the New York Botanical Garden as part of a special exhibit on Roberto Burle-Marx. A video highlighting the work of AF BIOTA members was put together during the COVID19 pandemic and is available in the BIOTA FAPESP YouTube channel (https://www.biota.org.br/dimensoes-da-biodiversidade-na-floresta-atlantica/). Short videos made by Ph.D. and Master's students associated with the project, which describe their work for the general public, are available in three languages (https://www.youtube.com/channel/UCF_n3stt5ImEoqv16L_Ndog).

4. *Conservation policy implications*

Several of our results and team members have helped conserve the AF biodiversity. For instance, our molecular phylogenetic and phylogeographic studies (Batalha Filho *et al*. 2014, Cabanne *et al*. 2007, 2008, d'Horta *et al*. 2013) were used to elevate former subspecies of three AF bird species to full species status (*Xiphorhynchus atlanticus*, *Conopophaga cearae*, and *Sclerurus cearensis*). With this information, three new globally endangered species were added to the Red List of Endangered Species (IUCN 2022). Moreover, biogeographic information produced by the team was used to help delimit conservation areas in the AF by the Brazilian Ministry of

Environment, during a meeting to discuss Targets for the Conservation of the Atlantic Forest biodiversity in Atibaia, SP, 2018. The phylogenetic diversity of highly endemic species of arachnids of the order Opiliones has been suggested as of special importance to assess conservation value (Nogueira *et al*. 2019a). US-based PI Carnaval edited the Americas Assessment Chapter at the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and was the editor of the Brazilian Platform on Biodiversity and Ecosystem Services report. PI Miyaki joined various meetings organized by the Instituto Chico Mendes para a Conservação da Biodiversidade (ICMBIO) from the Brazilian Ministry of Environment, helping to plan conservation actions for various endangered species. PI Miyaki and postdoc Bertola joined the Conservation Genetics Specialist Group of the International Union for Conservation of Nature in 2017.

Conclusions

Amongst the lessons learned, we found that integration of data across different fields of knowledge was (and still is) a considerable challenge in projects of this nature. As an example, the comprehension of technical terms that are specific to Biology was sometimes a difficult task for geologists and engineers, and vice versa. This is reflected by the fact that we only succeeded to publish papers that involved true integration of fields and data five years after the onset of the grant, with several manuscripts still being produced. Because such projects are so challenging, it is important that these grants last for more than five years and allow for true convergence across research groups, as ours did. As young researchers (graduate students and postdocs) participated in our meetings and were in close contact with our diverse group of laboratories and more senior investigators, they had the opportunity to experience this exchange and cross this gap. This new generation of researchers will unquestionably be better prepared to navigate among different scientific fields.

Unfortunately, the preservation of biodiversity is not the priority of many governments worldwide. As of our publication date, is likewise not a priority of the Brazilian government. While the future of Brazilian biodiversity seems grim, the AF deserves to be conserved. Even with so little vegetation cover, it still holds an immense and telling diversity of life forms, providing ecological and evolutionary services to the country and the globe. Based on the success story of this project, we strongly recommend that FAPESP continues to support research focused on Brazilian biodiversity, in particular, on hotspots, such as the AF. To effectively conserve this precious biome, home to the majority of the Brazilian human population, and leverage the work done by AF BIOTA, it will be important to invest in studies that combine our understanding of the processes that generate, maintain and erode the AF biodiversity with the social, cultural, environmental and economic needs of the Brazilian people. This is the next level of integration that we are missing.

Supplementary Material

The following online material is available for this article:

Supplementary 1 - List of Atlantic Forest new species described by members of the AF Biota project.

Supplementary 2 - List of papers published on phylogeography of Atlantic Forest taxa.

Supplementary 3 - List of papers published with phylogenies including taxa that occur in the Atlantic Forest.

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Associate Editor

Carlos Joly

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study did not involve human beings and/or clinical trials that should be approved by one Institutional Committee.

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