The Cerrado once connected the Andes with the Atlantic Rainforest

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Bird species *Syndactyla rufosuperciliata*. A genetic and computational analysis of birds suggests that the Andean and Atlantic tropical forests, which are now almost a thousand kilometers apart, were connected via the Cerrado in the distant past. Credit: Gustavo Cabanne

The tropical forests of the Andes and Brazil's Atlantic Rainforest biome are separated by almost 1,000 km of drier areas with open vegetation in the Chaco, Cerrado (Brazilian savanna), and Caatinga (Brazilian semiarid) biomes. Today, these tropical forests are not connected, but the fact that they share closely related species and lineages suggests that

these biomes were connected in the past. For example, 23 rainforest bird species have been found in both the Andean and Atlantic tropical forests.

Several published studies reinforce such hypothesis. What scientists do not know for sure is whether this connection consisted of past gallery forests along rivers in what is now the Chaco (which spans across southern Bolivia, northern Argentina and Paraguay) or the Cerrado (in part of Bolivia, central-west Brazil and northern Paraguay).

According to a new study based on genomic and biogeographical data for two bird species (Syndactyla rufosupercilita and S. dimidiata), the past connection between Andean and Atlantic tropical forests ran through the Cerrado. Such connection may have emerged several times during the Pleistocene, the geological epoch that lasted from approximately 2.5 million years ago to 11,700 years ago.

The study was part of a research project conducted by Gustavo Cabanne, an ornithologist at Argentina's Museum of Natural Sciences (MACN), in collaboration with Cristina Yumi Miyaki, a professor at the University of São Paulo's Bioscience Institute (IB-USP) in Brazil. Results of the study were published in the journal *Molecular Phylogenetics and Evolution*.

Biogeography is the study of the relationships among living beings, latitude, elevation and climate over time. Paleobiogeography focuses on species distribution and relationships in remote epochs. An understanding of the paleobiogeography of the species that inhabit certain biomes in the present can help scientists infer the distribution of these same biomes in the past.

"The main challenge in biogeographical research is integrating and interpreting the information obtained from several sources, such as data

on biological components and genomes for the species analyzed, geology and paleoclimate, palynology [pollen and spores], and even remote sensing data from satellite imagery," Miyaki said.

"We needed to collect and analyze all these kinds of data in order to investigate the hypothesis that there was an ancient connection between the Andean and Atlantic tropical forests and to test whether this connection ran through the Cerrado or the Chaco. The connection may have consisted of gallery forests that, during the Pleistocene, would have been remnants of wetland vegetation crossing more arid biomes."

According to Cabanne, the existence of a connection between the Andean and Atlantic tropical forests is supported by palynological studies, among others, according to which both forests expanded transitorily in some regions (such as the Cerrado) toward the Andes during the most recent glacial cycle and last glacial maximum, i.e., the coldest period among the various ice ages that occurred in the past 2.5 million years (at least 11 have been identified).

"In this past biogeographical context, the Andean and Atlantic tropical forests may have served as refugia. Their dynamic history [connection and isolation cycles] may have been an important driver of speciation in the Neotropics [a region comprising Central and South America, the Caribbean and parts of Mexico and the United States]," Cabanne said.

In the present interglacial period, Cabanne explained that these biomes represent forest refugia, where isolated organisms in either biome are expected to differentiate. During the Pleistocene ice ages, both forests were connected, allowing for gene flow between forest domains.

Genetic and computational analysis

In the study published in *Molecular Phylogenetic & Evolution*, researchers

chose to study the Buff-browed Foliage-gleaner, a New World ovenbird whose scientific name is Syndactyla rufosuperciliata, a passerine belonging to the order Passeriformes and family Furnariidae, as do other ovenbirds, such as the Rufous hornero (Furnarius rufus) and 230 other species found in Argentina, Bolivia, Brazil, Ecuador, Paraguay, Peru and Uruguay. There are five recognized subspecies in this taxon.

"S. rufosuperciliata is an appropriate model with which to explore the Andean-Atlantic forest connection because it inhabits both the main forest domains and the areas that could have been directly involved in bridging them: the gallery forests of the eastern Chaco and some parts of the southern Cerrado," Cabanne said.

Researchers used niche modeling to investigate the historical connectivity between the two regions. They then used DNA sequences from 71 birds and the genomic analysis of samples from other 33 specimens to evaluate the genetic structure of the population and the gene flow within the species. Lastly, they performed population model selection with the aid of approximate Bayesian computation (ABC), a method of inference based on summary statistics.

According to the researchers, their genomic analysis showed that the populations of S. rufosuperciliata now found in the Andean and Atlantic tropical forests belong to different lineages, but hundreds of thousands of years ago, the species was far more widely distributed, and its lineages were less differentiated from a genomic standpoint.

As the ice age continued and the vegetation in the Cerrado advanced and retreated, Andean and Atlantic birds became isolated from each other for tens of thousands of years, leading to diversification into two lineages.

The data also suggested new contacts between the eastern and western

populations of the species during the interglacial periods of the Pleistocene, when temperatures rose and rainforests advanced, permitting cross-breeding between the two lineages and new gene exchanges.

The analysis of genomic diversity between Andean and Atlantic birds combined with paleoclimate data suggested that these gene exchanges occurred via the Cerrado to the north rather than via the Chaco further to the south.

"Our results showed that the Andean and Atlantic tropical forests were refugia and that populations of the species from both regions made contact via the Cerrado," Cabanne said. "This suggests that the historical dynamics of the Andean and Atlantic forests played an important role in the evolution of forest birds in the region."

"Our findings are consistent with studies of other organisms and may indicate a more general pattern of connectivity among biomes in the Neotropics," Miyaki added.

In addition, this new study and previous research by the same group "point to high levels of cryptic diversity [meaning morphologically similar but genetically diverse species] between the Andes and Atlantic Rainforest biomes and suggest that the Andean population of S. rufosuperciliata should be recognized as an independent species," Cabanne added.

More information: Gustavo S. Cabanne et al, Phylogeographic variation within the Buff-browed Foliage-gleaner (Aves: Furnariidae: Syndactyla rufosuperciliata) supports an Andean-Atlantic forests connection via the Cerrado, *Molecular Phylogenetics and Evolution* (2019). DOI: 10.1016/j.ympev.2019.01.011

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