


# A multidisciplinary overview on the Tupi-speaking people expansion

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## Abstract

The cultural and biological diversity of South American indigenous groups represent extremes of human variability, exhibiting one of the highest linguistic diversities alongside a remarkably low within-population genetic variation and an extremely high inter-population genetic differentiation. On top of that, this region has seen some of the most dramatic demographic events in human history unleashed by the European colonization of the Americas. As a result of this process, the distribution of indigenous populations has been radically changed. In this review we focus on the Tupi, the largest and most widespread linguistic family in eastern South America. Tupi are believed to have originated in southwestern Amazon, from where some of its subfamilies expanded into other parts of the Amazon and, in the case of the Tupi-Guarani, beyond its borders. Recent evidence from archaeology, linguistics, and genetics aligns with José Brochado's Tupi Expansion model. He proposed that the gradual development of agricultural systems within the Amazon resulted in population growth and, eventually, territorial expansion. This model also supports separate Tupi Expansion branches: Tupinambá (Atlantic coast) and Guarani (south, midwest Brazil). Although being the most populous group on Brazil's Atlantic coast, which was the most affected by European colonization, the Tupi still account for roughly 20% of the country's overall indigenous population. Finally, despite its importance and more than a century of research on the Tupi and their expansion history, many key questions remain unanswered, which we attempt to summarize and explore here.

## KEYWORDS

archeology, demographic expansions, genomics, linguistics, Tupi

## Abstract in Portuguese

A diversidade cultural e biológica dos grupos indígenas sul-americanos representam extremos da variabilidade humana, abrangendo uma das maiores diversidades linguísticas e uma das menores diversidades genéticas intrapopulacionais do mundo, assim como uma das maiores diferenciações genéticas interpopulacionais. Além disso, esta

Towards a biocultural synthesis of the peopling of the Americas

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região presenciou alguns dos eventos demográficos mais dramáticos da história da humanidade, desencadeados pela colonização europeia das Américas. Como resultado desse processo, a distribuição das populações indígenas mudou radicalmente. Nesta revisão, focamos nos Tupi, o maior e mais difundido grupo linguístico do leste da América do Sul, dentre as sete principais famílias linguísticas do continente. Acredita-se que os Tupi tenham se originado no sudeste da Amazônia, de onde algumas de suas subfamílias se expandiram para outras partes da Amazônia e, no caso dos Tupi-Guarani, para além de suas fronteiras. Evidências recentes da arqueologia, linguística e genética alinham-se com o modelo de Expansão Tupi de José Brochado. Ele propôs que o desenvolvimento gradual dos sistemas agrícolas na Amazônia resultou no crescimento populacional e, eventualmente, na expansão territorial. Esse modelo também apóia ramos separados da Expansão Tupi: Tupinambá (costa atlântica) e Guarani (sul e centro-oeste do Brasil). Embora sejam o grupo mais populoso da costa atlântica do Brasil, que foi a mais afetada pela colonização europeia, os Tupi ainda representam cerca de 20% da população indígena total do país. Finalmente, apesar de sua importância e de mais de um século de pesquisa sobre os Tupi e sua história de expansão, muitas questões-chave permanecem sem solução, as quais tentamos resumir e explorar aqui.

## 1 | INTRODUCTION

The human history and diversity in South America are unique when all their biological and cultural dimensions are considered. This region encompasses both the greatest linguistic diversity, regarding the number of genealogical units, along with the proportion of language isolates (languages with no genealogical relatives) and small linguistic families (Michael, 2021). Despite this, South America is home to some of the living populations with the lowest within-population genetic variability—and the highest homozygosity and identity by descent levels—in the world (Bergström et al., 2020; Castro e Silva et al., 2022).

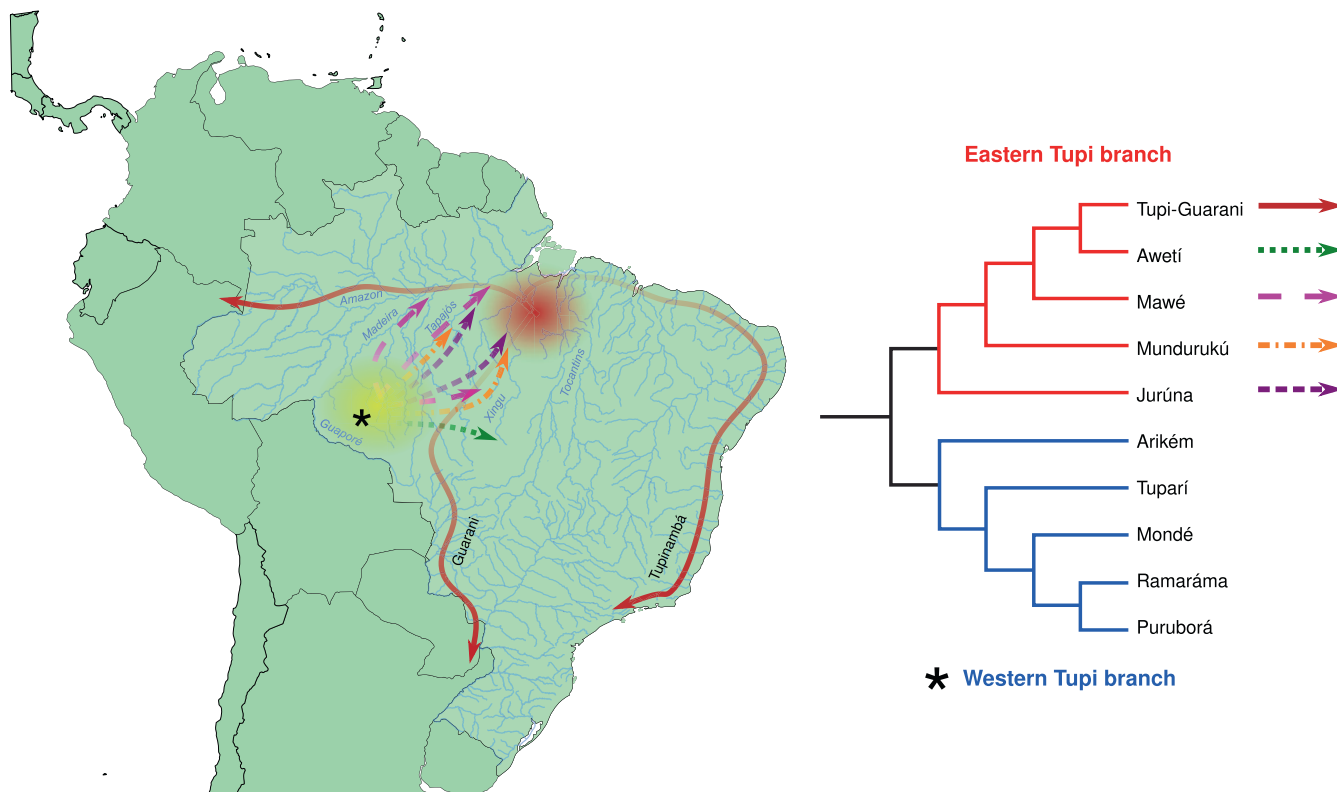
Furthermore, over the last five centuries, American Indigenous peoples have experienced some of the most dramatic and abrupt demographic changes in human history, including the extermination of more than 90% of the native population and widespread admixture with European colonizers and enslaved African people forcibly brought during the Transatlantic Slave Trade (Adhikari et al., 2017; Castro e Silva et al., 2022; Ongaro et al., 2019).

Despite the low genetic diversity, seven large language families originated in South America (which include six or more genealogical units, for more details, see (Campbell, 2012; Michael, 2021)), namely: Arawak, Karib, Macro-Jê, Pano, Quechua, Tukano and Tupi. Apart from these major linguistic groups, South America has 48 small linguistic families and 53 language isolates, with roughly 420 languages currently spoken (Campbell, 2012; Michael, 2021). For instance, these

include noteworthy small linguistic families such as the Aymara (Andes), Chon (Patagonia), Guaikuru (northern Argentina, western Paraguay, and southern Brazil), and Yamomámi (northwestern Amazon) (Campbell, 2012). This makes South America one of the world's most linguistically diverse regions.

Regarding the number of languages, Tupi stands as the largest linguistic family in eastern South America and ranks as the second largest across South America, behind only Arawak (Campbell, 2012). However, it is worth noting that Arawak has extended its presence into the Caribbean region as well. Furthermore, it is important to highlight that other linguistic families like Quechua, while encompassing fewer languages, have significantly larger numbers of speakers (Michael, 2021). Besides its large number of speakers, the Tupi groups represent one of the largest demographic expansions in human history, peopling a vast part of South America (Castro e Silva et al., 2020; Gregorio de Souza et al., 2020; Michael, 2021; Noelli, 2008).

In the first section of this review, we provide an introduction to the Tupi linguistic family, encompassing its diversity and pre-Columbian geographical distribution. We then examine the evidence concerning the origins of Tupi and its correlation with a distinct “Tupiguarani” ceramic tradition (characterized by ceramics painted in red and black colors on white clay). Moreover, we evaluate the contemporary distribution and diversity observed among present-day Tupi speakers and descendant populations, and how it has been shaped by the dramatic effects of the European colonization.



**FIGURE 1** Expansion of Tupi linguistic subfamilies. The yellow and red shaded areas, between the Madeira and Guaporé rivers, and the Xingu and Tocantins rivers, represent the Tupi and Tupi-Guarani's hypothesized centers of origin, respectively. The arrows illustrate very broadly the general expansion routes of the five Tupi linguistic subfamilies that have moved outside the Madeira-Guaporé region (i.e., Eastern Tupi branch), which are color-coded as indicated in the phylogeny of Tupi languages shown on the right panel (Rodrigues, 2012). The asterisk indicate the Tupi linguistic subfamilies that have remained in the Madeira-Guaporé region (i.e., Western Tupi branch) (Rodrigues, 2012). Country borders are drawn to enhance comprehension of particular regions.

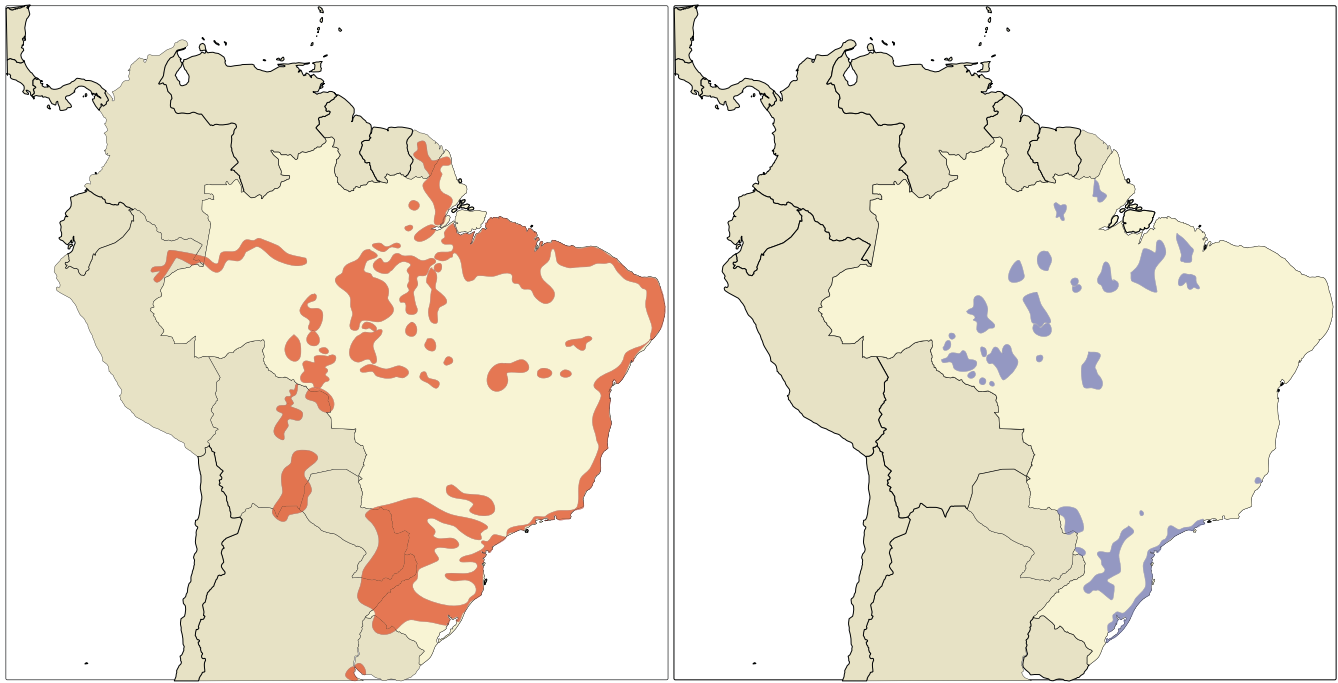
In the second and third sections, we attempt to shed light on key questions regarding the Tupi expansion process, which remain at least partially unresolved despite decades of research. Particularly in relation to some crucial aspects: (i) triggering factors and main hypotheses for the expansion; (ii) genetic continuity and relatedness between the Tupi-speakers and speakers of other linguistic families (e.g., Arawak, Jê, and Karib). We review these topics considering whether historical linguistics, population genetics, cultural anthropology, and archaeology all tell the same story.

## 2 | TUPI ORIGINS, DIVERSITY AND DISTRIBUTION

The Tupi linguistic family was widely distributed across South America when Europeans first arrived, encompassing not only the current territory of Brazil, but also neighboring parts of Argentina and Paraguay in the south, Bolivia and Peru in the west, and French Guyana in the north. Tupi speakers are essentially Amazonian peoples who originated and adapted to forest life, especially to riverine forest environments. However, one of its branches spread outside the Amazon, to the south and east, populating the Parana Basin (Guarani) and the

Atlantic coast (Tupinambá) (Figure 1). The names Guarani and Tupinambá identify both the peoples and their languages. When Europeans first arrived in the lands that would become Brazil, these were the first peoples to come into contact with them, and Tupinambá were, at this point, the largest indigenous coastal group. Scholars such as the Spanish abbot Lorenzo Hervás y Panduro, in his *Catálogo de las Lenguas de las Naciones Conocidas*, noticed and highlighted linguistic and cultural similarities between these groups, which later motivated their unification into a single linguistic group, the Tupi-Guarani (Rodrigues, 2012; Urban, 1992).

Currently, the Tupi linguistic family can be divided into 10 subfamilies that cluster languages with greater similarity and/or closer common ancestors, all of which, with the exception of the Tupi-Guarani, have remained confined within the Amazonian forest (Michael, 2021; Rodrigues, 2012) (Figure 1). Other linguists classify Tupi languages into a distinct number of subfamilies (e.g., Galucio et al., 2015; Jolkesky, 2016; Meira & Drude, 2015), which is partially due to methodological differences (for a detailed examination of the historical classification of Tupi languages please refer to Michael (2021)). The Tupi-Guarani is the most diverse and geographically widespread of these subfamilies, with speakers ranging from the Brazilian Atlantic coast to the south of Brazil and Paraguay, and all the way up to the



**FIGURE 2** Pre-contact and contemporaneous distribution of the Tupi. The map on the left depicts the distribution of the Tupi before the European contact in South America (Iriarte et al., 2017), while the map on the right shows the current distribution of the Tupi in Brazil (“Povos Indígenas No Brasil—Instituto Socioambiental,” 2023). Country borders are represented to improve recognition of specific locations.

western Amazon, even though only two languages, Guaraní and Tupi-nambá, have spread outside the Amazon (Figure 2) (Michael, 2021), which is estimated to have happened around 2500–1700 years ago, after the Tupi-Guaraní linguistic family originated (Ferraz Gerardi et al., 2023; Noelli, 2008; Rodrigues, 1958, 1964).

Other linguistic subfamilies, however, have spread within the Amazon, with the Mundurukú going eastwards to the Tapajós and Xingú rivers, the Mawé also moving eastwards and to lower Madeira and Tapajós rivers, the Jurúna dispersing to the Tapajós and Xingú and finally, the Awetí advancing to the upper Xingú (Figure 1). Only the Arikém, Mondé, Puruborá, Ramaráma and Tuparí remained in Tupi’s presumed motherland, in southwestern Amazonia (Figure 1). Notably, this division between language groups that remained or departed the place of origin prompted linguists Aryon Rodrigues and Ana Suely Cabral to propose splitting the Tupi into two primary branches, the Western and Eastern Tupi branches (Figure 1) (Rodrigues, 2012).

Tupi’s extensive geographic distribution has historically caught the attention of archeologists and linguists, who have long suggested that they came from a single ancestral homeland (Noelli, 2008). It is worth noting again that the term Tupi is also used to refer to the people who speak these languages, which conflates the concepts of a Tupi language (and/or culture) and a Tupi people. In other words, this broad use of the term Tupi assumes that the Tupi language expanded alongside the people from its center of origin, while dismissing the possibility that the former simply spread to neighboring populations along the way. However, there is currently strong evidence, including genetic analyses from living indigenous populations, indicating that

the Tupi expansion occurred as a demic diffusion (Castro e Silva et al., 2020; Ramallo et al., 2013), which will be discussed in the next section.

Several lines of evidence point to a region between the Madeira and Guaporé rivers in southwestern Amazonia (known as the Madeira-Guaporé region), as the most likely common center of origin of all Tupi (Figure 1). More specifically, this region contains the largest concentration of Tupi languages, including five of the 10 Tupi subfamilies (Western Tupi branch; Figure 1), and also Tupi-Guaraní language speakers (Rodrigues, 2012; Walker et al., 2012). The genetic diversity estimated using various types of genetic markers is higher throughout Tupi populations from the Madeira-Guaporé region than in those from elsewhere (Ramallo et al., 2013; Rodrigues, 2012; Santos et al., 2015). Beyond that lexicostatistical analyzes along with the most supported archeological models (as discussed later) indicate this region as the center of origin (Brochado, 1984; Noelli, 2008; Rodrigues, 1964; Walker et al., 2012). For instance, phylogenetic analysis of Tupi languages shows that the earliest clades to diverge are located in the Madeira-Guaporé region (Walker et al., 2012). Taken together these evidences support the region as the most probable center of origin of the Tupi.

Identifying the center of origin of the Tupi is a critical first step in understanding its expansion and the consequences of this event. In this sense, according to the same rationale applied for the Tupi, the Tupi-Guaraní are believed to have originated in a region of eastern Amazonia between two large rivers, the Xingu and the Tocantins, that has the most linguistic and material culture diversity (Figure 1) (Almeida et al., 2015; Souza Mello & Kneip, 2017). Furthermore, the

application of linguistic migration theory to a bayesian phylogenetic classification of the Tupi-Guarani subfamily (Michael et al., 2015) gives compelling evidence for a northeastern Amazonian origin (O'Hagan et al., 2019).

Furthermore, this linguistic group has been linked to the Tupi-guarani ceramic tradition (Corrêa, 2014; Gregorio de Souza et al., 2020; Neves, 2011; Noelli, 2008). However, because some archeologists want to emphasize that groups who produced this type of ceramic did not necessarily speak Tupi-Guarani languages, the names of the material culture tradition (Tupiguarani) and the linguistic subfamily (Tupi-Guarani) are spelled differently. In other words, although the match between the material culture distribution and the historical distribution of the languages is almost exact, it is impossible to verify whether or not the Tupiguarani pottery makers were Tupi-Guarani language speakers (Brochado, 1984; Corrêa, 2014; Melatti, 2007). This ceramic tradition is dispersed through a large portion of the eastern South America lowlands, including the Amazon, the Cerrado in central Brazil, parts of the Caatinga in northeastern Brazil, the Mata Atlântica in the Brazilian south and southeast, the majority of the Brazilian Atlantic coast, and even some regions of the Argentine Pampas (Gregorio de Souza et al., 2020; Noelli, 1998, 2008).

In the last five centuries, the European invasion and colonization of South America led to dramatic demographic changes in the distribution and diversity of indigenous populations, first by the extermination of more than 90% of the populations, secondly by the admixture of the indigenous populations with new coming European and African peoples (Adhikari et al., 2017; Chacón-Duque et al., 2018; Ongaro et al., 2019). Similarly, linguist Aryon Rodrigues, one of the foremost scholars to study South America languages in the twentieth century, estimated that 75% of indigenous languages spoken by peoples from the land that would become the Brazilian territory have vanished, arguing that the remaining languages in the east of Brazil were so few that they could be counted on one hand's fingers (Aryon Dall'igna Rodrigues, 1994; Storto, 2019). As a consequence of these events, the current picture of the main South America ethno linguistic diversity and distribution, and particularly for the Tupi, has been completely reshaped (Figure 2).

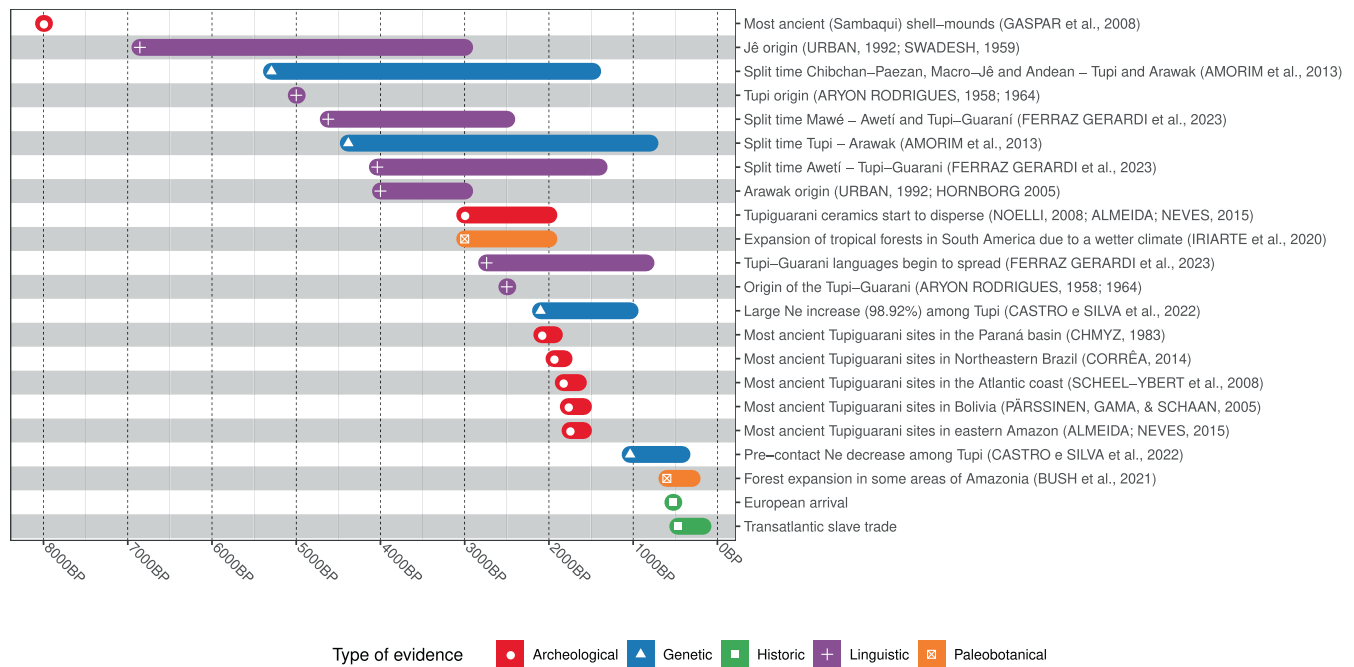
The genetic evidence indicates that Amazonian indigenous populations, including the Amazonian Tupi, were also subjected to severe population declines (Castro e Silva et al., 2022). However they have been less affected by the extensive admixture that indigenous populations have experienced since the European arrival (Castro e Silva et al., 2022). This indicates that despite facing similar reductions in effective population size, Amazonian indigenous communities likely had fewer direct interactions with Europeans and the broader Brazilian population in later periods. A scenario that would have contributed to decreased levels of admixture. In any case, the inferred reduction in effective population size ( $N_e$ ) for South America's linguistic family groups is enormous; for instance, the Tupi faced a  $N_e$  decline of 98.93% following European contact, a figure only exceeded by the inferred reduction for Mesoamerican indigenous populations

(Castro e Silva et al., 2022). It is noteworthy that changes in the  $N_e$  are only partially related to changes in the census size of a population (i.e. total number of individuals), as it is also influenced by other factors such as sex ratios, age structure, and non-random mating. The effect of these other factors certainly contributed to reducing even more the  $N_e$  of these populations, implying that the decline in census size during this period might have been comparatively less pronounced.

Brazil contains 154 indigenous languages, according to the mutual intelligibility criterion, with an estimated 230,000 indigenous language speakers (Moore, 2011). Conversely, according to the 2010 Brazilian Census ("Instituto Brasileiro de Geografia e Estatística—Indígenas," 2010), the indigenous population summed 817,963 people in the country. This demonstrates that a large proportion of indigenous populations (71.88%) no longer speak their native languages, a trend that is expected to worsen due to a number of factors, including indigenous children often not learning their native languages and historical prejudice against indigenous peoples, which discourages them from learning and using their languages (Storto, 2019).

The Tupi in Brazil, in particular, accounted for 156,073 (19.09%) of the total indigenous population in the country, and can be split into 51 separate ethnic groups, which can be clustered in 10 linguistic subfamilies Rodrigues, 2012. Overall, Tupi linguistic subfamilies encompass approximately 70 languages found throughout Brazil and neighboring countries, which are mostly concentrated in the Amazon, and the Tupi-Guarani subfamily includes 45 of these languages (Michael, 2021). In Brazil the Tupi-Guarani comprises 32 of the 51 Tupi ethnic groups and 120,978 (77.51%) individuals of the total Tupi population ("Povos Indígenas No Brasil—Instituto Socioambiental," 2023).

Noteworthy, the most recent data from the 2022 Brazilian Census (de Geografia e Estatística, 2023) reveals a significant 88.8% increase in the indigenous population in comparison to the last census, now constituting 0.83% of the total Brazilian population, totaling 1.69 million individuals. This notable rise can be attributed, at least in part, to a shift in the census methodology employed by IBGE. Previously, certain indigenous individuals identified themselves as "pardo" (a term denoting mixed-race individuals in Brazil), as the category "indígena" (indigenous in Portuguese) was provided as an alternative response to the question "qual é a sua cor?" (literally translating to "what is your color?"). Under the updated methodology, IBGE introduced an additional question, "você se considera indígena?" ("do you consider yourself indigenous?"), likely contributing to an increase in the number of self-identified indigenous individuals. Also noteworthy, various South American countries employ distinct criteria to identify indigenous individuals, which differ at least partially from the approach used in Brazil. The comparison between the 2010 and 2022 IBGE censuses in Brazil emphasizes that even minor differences in census methodologies can lead to significant variations in estimated numbers. Consequently, directly comparing estimates from different countries is challenging due to these methodological differences.



**FIGURE 3** Timeline of major events in Tupi history. The timeline is organized chronologically, presenting historical events based on inferred starting dates. Events are color-coded based on the type of supporting evidence. The x-axis represents time in years before present (BP), and the y-axis features brief event descriptions along with the respective references.

### 3 | TUPI EXPANSION: TRIGGERING FACTORS AND HYPOTHESES

Before talking specifically about how and why the Tupi dispersed from their centers of origin, we need a few words about the kind of movement that led to the extensive distribution of the Tupi. Archeological and ethnobiological data indicates that Tupi settlements were occupied and used for extended timespans, with dispersions into adjacent areas occurring without abandonment of the original territories (Brochado, 1984; Noelli, 2008). This evidence indicates that the Tupi expanded from their original territories, in opposition to a migration movement, where a territory is abandoned in favor of a new one. The causes of this expansion are still not completely understood, but we now have important pieces of information to assemble the puzzle of what caused it, as will be further discussed below.

Glottochronology and absolute dating provide the most reliable information for deriving a chronology of the Tupi expansion from its Amazonian origin (Noelli, 2008). In this sense, early glottochronological dating analysis of the Tupi languages indicated that Proto-Tupi must have originated around 5000 years ago (Arion D. Rodrigues, 1958; Rodrigues, 1964) (Figure 3), a timeframe that roughly corresponds to the inferred origins for other major linguistic groups, such as the Arawak and Jê, which are dated to 3000–4000 years ago (Hornborg, 2005; Urban, 1992) and 3000–6856 years ago (Swadesh, 1959; Urban, 1992), respectively. In turn, the Tupi-Guarani formation is dated to sometime around 2500 years ago (Ferraz Gerardi et al., 2023; Rodrigues, 1958; Rodrigues, 1964) (Figure 3).

The inferred linguistic split dates also approximately coincide with those obtained for the genetic split times inferred between the speakers of these linguistic groups, as determined by the application of the Approximate Bayesian Computation (ABC) approach to 381 autosomal STRs from five populations of speakers of languages representing 5 of South America's largest linguistic groups (Amorim et al., 2013). The inferred split time in the best fitted model for the Chibchan-Paezan, Macro-Jê, Andean (Aymara and Quechua), and a branch including Tupi and Arawak was 3094 (1480–5294) years ago (Amorim et al., 2013) (Figure 3).

Considering the estimated linguistic divergence times, it becomes apparent that the Tupi-Guarani expansion was remarkably rapid. This is evident when aligning these linguistic splits with corresponding archeological evidence for the early presence of Tupiguarani ceramics in several regions (Figure 3): Eastern Amazon:  $1670 \pm 80$  years ago (Almeida et al., 2015); Bolivia:  $1680 \pm 90$  years ago (Pärssinen et al., 2005); Atlantic coast:  $1740 \pm 90$  years ago (Scheel-Ybert et al., 2008); Northeastern Brazil:  $1880 \pm 60$  years ago (Corrêa, 2014); Paraná Basin:  $2010 \pm 75$  years ago (Chmyz, 1983). Therefore, possibly within a period of much less than 1000 years, the Guarani were already present in the Brazilian states of Paraná and Rio Grande do Sul and the Tupinambá in Piauí, Rio de Janeiro, and São Paulo (Figure 2).

However, due to the chronological proximity between the early presence of Tupi at the boundaries of their territorial expansion, as evidenced by these oldest absolute dates, and the inferred starting period for the Tupi-Guarani differentiation approximately 2500 years ago (Ferraz Gerardi et al., 2023; Rodrigues, 1958; Rodrigues, 1964)

(Figure 3), it has been argued that this timeframe has likely been underestimated (Noelli, 2008). This implies that previous linguistic analyses would have underestimated the temporal depth of Tupi-Guarani origin, leading for instance to wrong expectations regarding the levels of linguistic differentiation among populations and also biasing hypotheses about the triggering factors of the expansion in favor of a more recent timeline, among other demographic history aspects. In any case, the absolute dates show that Tupi-Guarani groups have been settling the outskirts of their territorial expansion range for at least 2000 years, establishing the antiquity of this population dispersal and occupation of these landscapes.

Several routes for the dispersal of the Tupi-Guarani, as well as the climatic, sociocultural, and/or demographic factors involved, have been proposed over more than a century of archeological, linguistic, historiographical, and ethnographic research. Anthropologist Alfred Métraux proposed a model based on historical data and historical linguistics, in which the Tupi-Guarani would have used the Amazon basin's extensive river connections to quickly disperse to the southern region and the Paraná basin. They would then have occupied the Atlantic coast from that region, which would have occurred only a few hundred years before Europeans arrived (Métraux, 1927).

It is noteworthy that the process, according to Métraux, would have taken the form of migrations, implying that the centers of origin would have been abandoned in search of new lands. This model was later reinterpreted to take climate change into account as a driving factor of the dispersal. The new interpretation argued that drier climates and forest fragmentation prompted a search for more suitable lands for these groups' lifestyles and livelihood strategies, and areas surrounding the southern Amazon would have acted as refugia for these populations, thus progressively pushing them to migrate to the Paraná basin, and beyond (Meggers, 1974, 1977, 1982; Meggers & Evans, 1978).

Conversely, archeologist Donald Lathrap proposed a "cardiac model" of Tupi-Guarani people dispersal based on linguistic, ethnographic, and, most crucially, archeological data. He hypothesized a gradual and slower radial spread from an Amazonian center of origin, also via river networks (Lathrap, 1970). This model was later improved by Brazilian archeologist José Brochado, who posited that the differentiation of languages and ceramic traditions was induced by the divergence and differentiation of the Proto-Tupi, which in turn was ultimately caused by continuous population growth in the central Amazon region due to agricultural food production (Brochado, 1984).

Given that the proposed event has the characteristics of a demic expansion, this implies that the Tupi-Guarani territories were not abandoned in the process; additionally, these groups would have expanded in a pincer movement from a dispersion center in southeastern Amazonia (according to the most recent evidence; (Almeida et al., 2015; Castro e Silva et al., 2020; Souza Mello & Kneip, 2017)), with one of the branches heading south and into the Paraná basin and the other to the east, following the Amazon River up to its mouth and then towards the Atlantic coast, which would have been occupied as far as the Cananéia region on the coast of São Paulo. The southern branch would have given rise to the Guaraní and the eastern branch to the Tupinambá (Figure 1).

In short, these two models have fundamentally different premises for understanding the dispersal of the Tupi-Guarani peoples, such as the way in which population movements occurred, the temporal depth of these events, and the triggering factors. At the same time, they agree that both languages and material culture were dispersed through population movement rather than simply cultural diffusion. Another point of agreement is that these dispersals would have occurred via river routes. This has been challenged by a series of evidences that show the Tupi-Guarani occupying and reoccupying *terra firme* (non-floodable lands) over long periods of time, particularly in the southeastern region of the Amazon, between the Tocantins and Xingu rivers, demonstrating that land routes must also be considered in models that seek to explain the phenomenon of the Tupi-Guarani expansion (Almeida et al., 2015).

The genomic analysis of present-day populations have shown that the autochthonous genetic component of the Tupiniquim, a small and admixed Tupi indigenous community from the Brazilian Atlantic coast, is most genetically similar to the Amazonian Tupi, and especially to the Amazonian Tupi-Guarani (Castro e Silva et al., 2020). Fundamentally, these findings demonstrate that the Tupiniquim and other coastal Tupi descended from Amazonian Tupi ancestors, and that the dispersal of Tupi-Guarani languages and material culture in the past can be explained by the dispersal of peoples who spoke these languages, rather than simply by cultural diffusion.

Indeed, population history models were generated using the Tupi Expansion hypothesis originally proposed by Métraux (Métraux, 1927) and Brochado (Brochado, 1984), and the statistical adjustment of the models was estimated, consistently demonstrating that models structured according to Brochado's hypothesis have a good fit and/or explain the data of the sampled populations significantly better (Castro e Silva et al., 2020). Taken together these results add to a growing body of evidence pointing to the occurrence of several demic diffusion processes in South America with origins in the Amazon (Gregorio de Souza et al., 2020).

Furthermore, a recent analysis of paleoecological and paleoclimatic data (Iriarte et al., 2017) supports a scenario that is very different from the one proposed by the archeologist Betty Meggers (Meggers, 1977, 1974, 1982; Meggers & Evans, 1978). Instead of drier climates and forest fragmentation, evidence points to the existence of a wetter climate in the Late Holocene, which would have led to the expansion of tropical forests in South America between 3000 and 2000 years ago, exactly during the hypothesized period of the Tupi Expansion's onset (Brochado, 1984; Noelli, 2008).

This expansion of tropical forests, particularly of riverine forests, would have provided an ecological opportunity for the Tupi-Guarani to expand by providing the necessary conditions for the specific type of food production they had previously mastered within the Amazon, known as polyculture agroforestry (Iriarte et al., 2020; Neves, 2013). This food production system combines the cultivation of domesticated plants with the management of semi-domesticated ones in the midst of forest environments, and was particularly associated with riverine forest environments (Iriarte et al., 2017). This is further supported by demographic models built to assess different simulated

climate change scenarios (Gregorio de Souza et al., 2020). This approach suggests that a demic-diffusion process primarily occurring within tropical moist forests aligns best with the archeological and linguistic timelines. The best models indicate a prolonged period of stasis in the Amazon, succeeded by a rapid emergence of Tupi branches and a swift expansion beyond the Amazon into various parts of eastern South America. As a result, this new evidence supports Brochado's model, including the hypothesized chronology, while also demonstrating the existence of additional factors that would have facilitated or possibly triggered the expansion process.

Archeologist Francisco Noelli argues that a number of pieces of evidence refute the hypothesis that the Tupinambá language and material culture are descended from Guarani (or Proto-Guarani) populations in the southern part of Brazil and the surrounding areas (Noelli, 2008). The argument can be summarized by two main points: the first is that given the absence of a material culture development sequence outside the Amazon (Brochado, 1984), the Tupinambá ceramic subtradition could not have developed outside the Amazon, and thus could not have spread in a south to north axis, as expected if derived from the Guarani subtradition. In light of this, there is no continuity between the Tupinambá subtradition and the material culture discovered in the lower geological layers in the regions where it can be found. Second, linguistic analysis indicates that Tupinambá is likely the earliest Tupi-Guarani language (Jensen, 1990), which also implies that it could not have evolved from the Guarani language branch and, consequently, that it could not have spread to the Atlantic coast from the region around southern Brazil. This is further corroborated by recent Bayesian linguistic phylogenetic analyses which have utilized extensive Tupi-Guarani language datasets (Ferraz Gerardi et al., 2023; Gerardi & Reichert, 2021). These analyses reveal a closer linguistic affinity between Tupinambá and Amazonian Tupi-Guarani languages, in comparison to Guarani, challenging the notion of a northward coastal movement for the Tupinambá.

Noelli also noted that the Tupinambá and Kokama languages have unique characteristics that distinguish them from other Tupi-Guarani languages spoken south of the Amazon River (Noelli, 2008). This closer relatedness to the Kokama would be evidence that the Tupinambá expansion came from the lower Amazon, again supporting a distinct origin from the Guarani. However, despite sharing a lot of lexical material with other Tupi-Guarani, the hypothesis of a Tupi-Guarani origin for the Kokama language has been rejected (Câmara Cabral, 1995; Michael, 2014). This is also supported by the analysis of genomic data from contemporary indigenous populations in South America has shown that present-day Kokama are actually more closely related to Arawak-speakers from their region (i.e., the western Amazon) than to other Tupi-speaking groups (Castro e Silva et al., 2022). This finding implies that the Kokama were originally Arawak speakers, or members of a closely related group, who underwent a process of linguistic replacement and adopted a Tupi-Guarani language. Therefore, specifically regarding the relationship between the Tupinambá and Kokama (at least the Kokama analyzed so far), genetic analysis cannot be used to traceback their center of origin and diversification.

Furthermore, demographic inferences of the Tupi based on the analysis of identity by descent (IBD) genomic segments demonstrates that in the period between approximately 2100–1000 years ago their effective population size had an increase of 98.92% (Castro e Silva et al., 2022) (Figure 3). This result demonstrates the occurrence of a population growth in the hypothesized starting period of the Tupi Expansion (3000–2000 years ago), as expected by the Brochado's model (Brochado, 1984). Surprisingly, this analysis of the IBD segments also show a reduction of the effective population size previous to the European-contact, starting from approximately 1000 to 400 years ago (Castro e Silva et al., 2022) (Figure 3), which partially overlaps with an inferred period of forest expansion between 600 and 300 years ago (Figure 3), indicative of human population decline (Bush et al., 2021). Nevertheless, as discussed by Castro e Silva et al. (2022), since eastern South America indigenous populations present on average short generation times in comparison to any other indigenous American groups (Coll Macià et al., 2021), the inferred starting time of the population collapse might be older if measured in terms of number of generations, as in this case.

Moreover, spatial autocorrelation analyses of mitochondrial genetic diversity of Tupi populations show that autocorrelations decrease with distance, a pattern consistent with isolation by distance and also suggestive of past demic expansions (Ramallo et al., 2013). In contrast, autocorrelations for Jê populations show no discernible pattern of constant increase or decrease with distance, which is consistent with a scenario in which there was no population expansion. The existence of a correlation between genetic and geographic distances among Tupi populations was also demonstrated by applying a Mantel test, which showed no significant correlation for the Jê populations (Ramallo et al., 2013).

Taken together, these pieces of evidences indicate that several factors contributed to the onset of the Tupi expansion. We now know that the combined effect of a Tupi food production system adapted to the Amazon environment (Jose Iriarte et al., 2020; Neves, 2013) and the ecological opportunity provided by a change to more humid climates, followed by forest expansions, played a crucial role to their expansion (Iriarte et al., 2017). However, we are still lacking information about the relative importance of these factors, and also whether other factors might have played a role in leading to the group's expansion, such as the social structure and the expansionist “ethos” of the Tupi-Guarani.

The Tupi-Guarani were socially organized into regional chiefdoms comprised of confederations of villages (Noelli, 1998). This societal structure enabled them to organize war expeditions that traversed great distances via major waterways. These expeditions had multiple objectives, including attacking enemies, annexing territories, capturing women, and, in some instances, enslaving the defeated (Santos-Granero, 2009). Central to the Tupi-Guarani culture was a strong bellicose ethos and a predatory cosmology. This found expression in practices such as anthropophagic ritual feasting, which carried significant social implications, particularly as a means of acquiring status, a practice that endured until colonial times (Fausto, 2012). Therefore, this expansionist ethos, deeply rooted in their culture and

societal structure, likely propelled the Tupi-Guarani to undertake territorial expansion, engage in conflict, and extend their influence across vast territories. This illustrates how the social and cultural characteristics of the Tupi likely played a role in driving the vast territorial expansion of the group.

#### 4 | GENETIC CONTINUITY AND RELATIONSHIPS AMONG THE TUPI AND ACROSS LINGUISTIC FAMILIES

It is also important to mention that the lands where the Tupi-Guarani spread into were not previously unoccupied. In fact, the Atlantic coast and some riverside areas had been inhabited by populations of fisher-hunter-gatherers who built shell-mounds (locally known as Sambaquis) since around 8000 years ago (Gaspar et al., 2008). Given the possibility that many shell mounds were built on the continental shelf that is now submerged beneath the Atlantic Ocean, the occupation could be even older. These Sambaqui groups would have occupied the Brazilian coast starting from around 8000 BP until the arrival of Tupi-Guarani groups and speakers of Macro-Jê languages, as evidenced by the presence of Tupiguarani and Taquara/Itararé pottery (a ceramic tradition associated with Jê-speaking populations from the south of Brazil) in the upper layers of some mounds (Gaspar et al., 2008).

Additionally, patterns of genetic similarity between modern-day indigenous populations and sambaqui individuals from some archaeological sites in the Brazilian Atlantic coast indicate a general closer relationship between Jê-speakers and Sambaqui people, even in comparison to the Tupiniquim, a Tupi Atlantic coastal population (Castro e Silva et al., 2020). In contrast to other linguistic groups, such as the Tupi, Jê-speaking groups in general exhibit higher genetic similarity with ancient Brazilians, indicating they may have a higher level of genetic continuity with ancestors from eastern South America (Castro e Silva et al., 2020). But this higher inferred similarity may be overestimated since the Jê-speaking communities included in that study are known to have had substantial inbreeding, leading to significant genetic drift effects that could confound inferences of allele sharing (Castro e Silva et al., 2020). These results are neither conclusive in favor nor against the possibility of some degree of admixture between the sambaqui peoples and the incoming Tupi-Guarani groups.

However, a recent comprehensive analysis involving 34 ancient individuals from coastal and riverine Sambaqui sites (Ferraz et al., 2023), marking the most extensive study of ancient Brazilians to date, revealed a notable temporal shift in genetic ancestry at the Sambaqui do Limão site along the coast of Espírito Santo state in southeastern Brazil. The study showed that older individuals dating back to 3200 and 2700 years ago displayed a stronger genetic affinity with the Jê-speaking Xavante from central Brazil. In contrast, the most recent individual dating to 500 years ago exhibited a higher genetic similarity with the Tupi-speaking Zoró from southwestern Amazonia. This genetic shift provides compelling evidence for the early presence of Tupi-speakers along the Atlantic coast. Furthermore, this suggests

a genetic connection between ancient individuals dating from around 3000 to 2000 years ago and Jê-speakers. This is reinforced by the observed genetic affinity with southern Jê-speakers in other individuals from the same time period, such as those from Jabuticabeira II, dating approximately 2200 and 1300 years ago (Ferraz et al., 2023). These results align with the proposed timeline of Jê-speaker dispersion from central Brazil to the southern and southeastern coastal regions. This dispersion is supported by the emergence of Taquara/Itararé ceramics in the southern coast approximately 3000 years ago and Una ceramics (another ceramic tradition associated with Macro-Jê-speakers) in the southeastern coast around 2000 years ago.

Regarding the genetic continuity, we still do not have any information about the relationship between ancient individuals associated with Tupi or Tupiguarani material culture and contemporaneous Tupi. Beyond that, we also do not know how the peoples that spread the Tupiguarani ceramic tradition to the south and the east are related to each other, to ancient Amazonians, and to present-day populations of these regions. In this sense, it is essential to study the genetic diversity of ancient individuals from eastern South America and the Amazon, which are still almost completely not represented in the genomic studies, with few exceptions (Ferraz et al., 2023; Moreno-Mayar et al., 2018; Posth et al., 2018).

To continue in the topic of ancient individuals, there is an almost complete absence of information about the interaction between the Tupi populations that have expanded from their Amazonian center of origin and the local peoples, at least in relation to the genetic outcome of these encounters. For instance, the analysis of ancient individuals will shed some light on whether these interactions with local populations led to some degree of admixture with local populations. Interestingly, as previously discussed, analyses have already shown that it is also possible for Tupi languages to spread through a cultural diffusion process, as evidenced by the Kokama people, which despite speaking a Tupi-Guarani language are more genetically similar to Arawak-speakers of the same region (Castro e Silva et al., 2022). This finding indicates that a linguistic replacement took place with the Kokama people, which are therefore most likely former Arawak-speakers who later adopted a Tupi-Guarani language. This prompts the question of how frequent this type of interaction between the Tupi-Guarani and local groups was throughout the Tupi Expansion process. Our capacity to answer this type of question would also greatly benefit from a better sampling and genetic study of both ancient and modern-day indigenous populations.

Despite the relevance of this knowledge, our understanding of the relationship between Tupi linguistic subfamilies and other linguistic groups, notably the three other major eastern South America language families, the Arawak, Karib, and Jê, remains quite limited. According to a recent study based on autosomal genetic variants, Amazonian Tupi and Karib-speakers are not genetically distinct, reflecting a history of contact and gene-flow (Castro e Silva et al., 2022). The potential connection between the Tupi-Guarani and the Karib linguistic groups is further supported by an extensive lexical material overlap (Rodrigues, 2014). As a result, processes that may sustain identity or cultural continuity in the face of cross-ethnic

interaction and migration are likely in action. However, it is possible that the resolution of the genetic data used in the referred study (SNP array) was insufficient to detect the existing genetic structure among the Amazonian Tupi and Karib, and that the future availability of complete genomes from these groups will allow us to address this issue.

At the same time, Macro-Jê-speaking communities, the largest indigenous linguistic group in Brazilian inlands, have a significantly distinct genetic profile not only in comparison to the Tupi, but also to any other eastern South America group (Castro e Silva et al., 2022). The genetic relationship between Tupi and Arawak speakers is also largely unknown. However, Arawak communities in western Amazonia seem to be more similar to populations from the same area, forming a distinct genetic cluster in comparison to indigenous populations to the west (Andes and Pacific coast), as well as to the east (Amazon and Atlantic coast) (Castro e Silva et al., 2022). Once again, a better representation of these indigenous communities in genomic studies will help to shed light on the relationship among and within different linguistic family groups.

The population history of the Tupi subfamilies is better understood. However, of the 51 Tupi-speaking ethnic groups, only 13 (representing four of the 10 Tupi linguistic subfamilies: Arikém, Guarani, Mondé, and Munduruku) have been studied through genome-wide studies, implying that a large piece of the puzzle is missing. With the exception of the Wajãpi and Kokama ethnic groups, the Tupi-Guarani subfamily forms a separate cluster from other Tupi (Castro e Silva et al., 2022) on a maximum likelihood tree calculated with Treemix (Pickrell & Pritchard, 2012) based on pairwise population genetic covariance. As previously stated, the Kokama are more genetically similar to Arawak speaking groups, thus forming a distinct branch with them (Castro e Silva et al., 2022). The Tupi Arikém and Tupi Mondé, both from southwestern Amazonia, form a single branch. In this branch Karitiana, which is the sole Arikém representative in that study, stands as the most basal ramification. Finally, there is no further clustering of the Tupi Munduruku inside the Tupi branch.

Current research indicates that when linguistic analyses are done on Tupi linguistic subfamilies, the general picture provided by genetic data is at least partially replicated. For instance, a distanced-based phylogeny based on a 40-vocabulary list from 48 Tupi languages (Walker et al., 2012) and a Bayesian phylogenetic analysis of lexical data from 30 Tupi-Guarani with two additional Tupi languages (Michael et al., 2015) reveal that Tupi-Guarani languages form a clade separated from other Tupi linguistic groups, mirroring Tupi-Guarani-speakers' genetic diversity in comparison to other Tupi-speakers. The first study, which included eight non-Tupi-Guarani Tupi languages (Walker et al., 2012), also allows us to compare the relatedness between different linguistic families and the genetic diversity of their speakers. In this comparison, the Arikém and Mondé are more distantly related to the Tupi-Guarani than Munduruku, for instance, indicating that there is at least some degree of correlation between genetic and linguistic distances (Castro e Silva et al., 2022).

Finally, the Guarani, which includes the Kaiowá, Mbyá, and Nãndeva ethnic groups, is the most genetically divergent branch within the Tupi-Guarani subfamily, with substantial mutual genetic similarity,

indicating a separate demographic history from the other Tupi (Castro e Silva et al., 2020; Castro e Silva et al., 2022). Besides that, the Guarani have most likely admixed with populations from the Chaco, contributing to the group's higher genetic distinctiveness (Castro e Silva et al., 2020, Castro e Silva et al., 2022). Conversely, the coastal Tupi represented by the Tupiniquim community from the southeast coast of Brazil, are more genetically similar to Amazonian Tupi and especially Amazonian Tupi-Guarani (Castro e Silva et al., 2020, Castro e Silva et al., 2022). As previously discussed, this is reinforced by closer linguistic affinities between Tupiniquim (Tupinambá) and Amazonian Tupi-Guarani, in comparison to the Guarani (Ferraz Gerardi et al., 2023; Gerardi & Reichert, 2021). This combined evidence strongly suggests an independent origin for the Tupinambá and Guarani.

## 5 | CONCLUSION

In this review, we have explored the origins, diversity, and dispersal of the Tupi. The Tupi were originally Amazonian peoples, deeply ingrained in the riverine forest environments. The Tupi-Guarani subfamily, the most diverse and widespread branch, holds connections from the Brazilian Atlantic coast to Paraguay and the western Amazon. The enormous dispersion of this linguistic subfamily, linked to the Tupiguarani ceramic tradition, is estimated to have started around 2500 years ago, underlining its significant role in South America's genetic and ethnolinguistic landscapes. Several lines of evidence suggest the Madeira-Guaporé region in southwestern Amazonia as the probable center of origin for all Tupi, while the Tupi-Guarani's origin is proposed in northeastern Amazonia.

This review also explores the triggering factors and hypotheses behind the Tupi expansion across the continent, revealing that this dispersion was a multifaceted interplay of demographic, cultural, and climatic dynamics, deeply influenced by the development of food production systems, ecological shifts, along with a unique social structure and an expansionist ethos. In this study, we present compelling evidence across multiple disciplines, including archaeology, linguistics, and genetics, that strongly supports Jose Brochado's model. According to this model, the Tupi Expansion was caused by the gradual advancement of food production systems within the Amazon, resulting in population growth and subsequent territorial expansion. Notably, our findings underscore that the Tupi populations along the Atlantic coast and the Guarani in the Brazilian south and midwest are distinct branches of the Tupi Expansion. This conclusion carries significant implications for understanding the relatedness between different Tupi-Guarani groups and sheds light on their history. Understanding this historical movement provides critical insights into the pre-Columbian history of South America and illustrates the intricate interplay of factors shaping the continent's linguistic, cultural, and genetic landscapes.

Lastly, this review sheds light on the intricate genetic dynamics and relationships within the Tupi population and their interactions with other linguistic and cultural groups across South America.

Despite valuable insights, significant gaps persist in understanding the cultural and genetic interactions between the Tupi-Guarani and other indigenous groups. In summary, this review underscores the importance, from a genetic perspective, of incorporating a more diverse array of indigenous populations and adopting an interdisciplinary approach to address these intricate questions. Such efforts are poised to deepen our understanding of Tupi genetics and ethno-linguistic landscapes, ultimately enriching the narrative of South America's ancient past and shedding light on the intricate relationships among its diverse indigenous populations.

#### AUTHOR CONTRIBUTIONS

**Tábita Hünemeier:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); writing – original draft (equal); writing – review and editing (equal). **Marcos Araújo Castro e Silva:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal).

#### DATA AVAILABILITY STATEMENT

No new data were generated.

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