

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Journal of Archaeological Science

journal homepage: <http://www.elsevier.com/locate/jas>

Delayed demographic transition following the adoption of cultivated plants in the eastern La Plata Basin and Atlantic coast, South America

Jonas Gregorio de Souza^{a,*}, Philip Riris^b^a Culture and Socio-Ecological Dynamics group, Department of Humanities, Universitat Pompeu Fabra, Spain^b Institute for the Modelling of Socio-Environmental Transitions, Department of Archaeology, University of Bournemouth, UK

ARTICLE INFO

Keywords:

Demography
Radiocarbon
Summed probability distributions
Agriculture

ABSTRACT

Understanding past population dynamics in lowland South America relative to changes in subsistence is crucial for drawing comparisons with global processes. Here, we use aggregated radiocarbon data as a palaeodemography proxy for in the eastern La Plata Basin and adjacent Atlantic coast, southeastern South America. Our results show that population dynamics in the study area are best explained by a three-phase model consisting of exponential growth ~6000-4000 cal BP, linear decrease ~4000-2000 cal BP and further exponential growth ~2000-500 cal BP. Local deviations from the regional trend show a heterogeneous landscape, with the first phase of exponential growth mainly driven by activity in the coast. Although the first adoption of domesticated plants occurs during that period, a causal relationship with population growth cannot be established, as plant cultivation may have been incorporated into the economy of already large and settled populations approaching carrying capacity. The second phase of exponential growth follows the arrival of new cultural traditions, bringing with them a more diverse package of cultivated plants and landscape management practises. Our results highlight the complexity of the relationships between population dynamics and changes in economy in South America, with a delayed transition attested in our study region.

1. Introduction

The transition from hunting and gathering to economies based on agriculture led to a major turn in human demography. In Eurasia, a dramatic growth in birth rates following the adoption of farming resulted in unprecedented population expansion, a phenomenon known as the Neolithic Demographic Transition (NDT) (Bocquet-Appel, 2011; Bocquet-Appel and Bar-Yosef, 2008). Originally, the NDT was inferred from bioanthropological data (Bocquet-Appel, 2002) and genetic clines in modern populations (Cavalli-Sforza et al., 1994), with population replacement during the spread of farming later confirmed by ancient DNA (Haak et al., 2010).

The mechanism that allowed farmers' population growth is much debated, with explanations mostly revolving around changes to fertility or increase in carrying capacity (Smith, 2015). In the first case, it is argued that fertility was raised as a result of higher caloric intake and lower energy expenditure with mobility, which allowed for shorter birth intervals (Bocquet-Appel, 2011). In the latter case, carrying capacity is argued to increase with the density and growth rate of resources – both of which are higher among plants and, especially, domesticated plants

(Bettinger, 2016). The chain of causation is inverted, with pressure on land leading to agriculture as a form of maximizing energy returns through higher labour input per unit of land (Bettinger, 2016; Boserup, 1965). Both explanations are not mutually exclusive: a positive feedback may be envisaged between intensification, raising of carrying capacity, and subsequent population growth – which demands further intensification.

More recently, statistical analyses of aggregated radiocarbon dates became a widely-employed method for assessing palaeodemography. The assumption behind such approaches is that relative population size will be reflected in the abundance of datable material and, consequently, on the number of radiocarbon determinations for a given period (Rick, 1987). Beyond the mere visual inspection of radiocarbon date frequencies, robust methods have recently been developed for explicit model testing. Most commonly, summed probability distributions (SPDs) of radiocarbon dates are compared to a null hypothesis, usually assuming uniform or exponential distributions, by means of Monte Carlo simulations (Timpson et al., 2014). This approach has the potential to identify significant peaks and troughs in the SPDs that are reflect change through time beyond sampling bias or artefacts created by the

* Corresponding author.

E-mail address: jonas.gregorio@upf.edu (J.G. de Souza).<https://doi.org/10.1016/j.jas.2020.105293>

Received 4 September 2020; Received in revised form 16 October 2020; Accepted 14 November 2020

Available online 10 December 2020

0305-4403/© 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

calibration curve. When applied to the large number of radiocarbon determinations spanning the Mesolithic and Neolithic in Europe, the use of statistical analyses of SPDs as a proxy for population dynamics found a common pattern: in different parts of the continent, the onset of the Neolithic was followed by rapid growth and subsequent decline - the latter potentially explained by outmigration, disease or overshooting of carrying capacity (Shennan et al., 2013; Timpson et al., 2014).

The question remains open, however, whether the same trajectory was followed in other parts of the world. In the Americas, few assessments of the relationship between changes in subsistence systems and population growth have been made, hindering an evaluation of the NDT as a global phenomenon. In North America, it has been argued that the continent as a whole does conform to the pattern of the NDT (Bocquet-Appel and Naji, 2006). However, some regions that have been subject to more rigorous analysis appear to have experienced a different process. For example, in the US Southwest, bioarchaeological data do not support a change in birth rates until ca. two and a half millennia after the introduction of maize cultivation (Kohler et al., 2008; Kohler and Glaude, 2008; Kohler and Reese, 2014). Significant population growth, it is argued, was not driven by the adoption of cultivated plants per se, but by a series of later developments: the arrival of more productive varieties of maize, the broadening of the agricultural package, and the establishment of sedentary villages (Kohler et al., 2008).

In the tropics of South America, it was hypothesized that the process of transition to agriculture and the role of domesticated plants in local economies differed markedly from those observed in Eurasia (Fausto and Neves, 2018; Neves, 2013; Shepard et al., 2020). A form of “cultivation without domestication” has been suggested by some researchers to be prevalent in the Neotropics, thus explaining the long delay between initial plant domestication and the transition to economies more heavily dependent on agriculture (Fausto and Neves, 2018). Polyculture agroforestry – the combination of low intensity cultivation of a broad range of domesticated species, management of (semi)domesticated trees, and formation of anthrosols – has also been argued to be a widespread economic pattern in tropical forest environments (Clement et al., 2015; Levis et al., 2017; Maezumi et al., 2018; Neves, 2007, 2013; Piperno and Pearsall, 1998). Intensive land use, however, was practised in some regions – as documented by raised fields, drainage canals and other productive infrastructure (Blatrix et al., 2018; Iriarte et al., 2012; Lombardo, 2010) – and there has been strong criticism of the view that pre-Columbian societies of the Neotropics were merely complementing their diets with a low intake of domesticated plants (Iriarte, 2009). Even in economies where agroforestry was dominant, the formation of anthrosols may be seen as a form of labour-intensive, long-term investment in the landscape, with the potential to support large populations in a sustainable manner (Iriarte et al., 2020).

Whatever the case, it is undeniable that agriculture in the Neotropics must be understood “on its own terms” and cannot be evaluated solely based on Eurasian standars (Denham et al., 2007). Although it would be incorrect to assume that Neotropical groups were mostly foragers who complemented their diets with a few crops (see criticism in Iriarte, 2009), it is also not necessarily the case that they were deriving most of their calories from domesticated plants or that they were practising field cultivation as Eurasian farmers.

Thus, given the different expansion capacities of agricultural systems worldwide (Harris, 2002), is it possible that the agroforestry economies of tropical South America resulted in a later onset of demographic expansions when compared to those of Eurasia? Or were the more intensive systems developed in the Neotropics capable of fostering rapid demographic growth? In this paper, we address that question with a regional case study, performing statistical analysis of aggregated radiocarbon determinations from the eastern La Plata Basin and adjacent Atlantic coast, one of the most intensely studied regions of lowland South America.

The application of formal model-testing to radiocarbon data with the aim of exploring prehistoric demography in South America is recent.

Population growth rates have previously been estimated by fitting a two-phase model to the continental SPD curve, showing logistic growth until ~5500 cal BP followed by a phase of exponential growth (Goldberg et al., 2016). In contrast with the expectations of the NDT, the transition between the two demographic regimes did not immediately follow the introduction of plant domesticates, but coincided with a trend towards increased sedentism (Goldberg et al., 2016). A more recent and complete assessment of the South American radiocarbon record has brought further evidence for a significant decline at the beginning of the mid-Holocene during a period of marked precipitation variability and aridity, followed by population recovery after ~6000 cal BP (Riris and Arroyo-Kalin, 2019). Renewed growth occurred in tandem with a broadening of the role of managed and cultivated plants in the economy, which may have mitigated the effects of drought (Riris and Arroyo-Kalin, 2019). For the initial occupation of South America, Prates et al. (2020) show that a logistic model better explains the continental SPD for the period ~15000-8000 cal BP. Significant positive deviations, however, appear to coincide with the Antarctic Cold Reversal stadial at 12500 cal BP, and with the emergence of specialised economies ~8400 cal BP (Prates et al., 2020).

SPDs for specific regions of South America have also been subject to explicit model-testing in order to assess population dynamics. For the Peruvian coast and highlands, for example, Riris (2018) has argued that sustained population growth occurred throughout the Holocene, except for an event of decline ~5000 cal BP. In the South-Central Andes, Gayo et al. (2015) found a decline in population levels ~9500-6000 cal BP, followed by rapid recovery. The coastal Atacama Desert, however, conformed to a different pattern, with stable (albeit low) population levels ~7800-6000 cal BP followed by a brief expansion and another event of decline ~5500-4550 cal BP (Gayo et al., 2015). For the Amazon Basin, Arroyo-Kalin and Riris (2020) have identified a phase of logistic growth starting ~1700 cal BP, an indication that Amazonian populations may have reached carrying capacity at the eve of the European encounter. The latter trend deserves special attention, as its onset follows by a few centuries the appearance of anthrosols (Amazonian Dark Earths or *terra preta*) throughout the basin (Iriarte et al., 2020), at least suggesting that intensive agroforestry systems may have enabled rapid population growth. However, given the spatial variability in demographic trajectories so far observed in South America, more regional case studies are necessary to evaluate local responses to changes in the subsistence system.

Here, we assess the radiocarbon record of the eastern La Plata Basin and Atlantic Coast (ELBAC), southeastern South America, as a proxy for population dynamics. By applying formal model-testing to SPDs, we compare the spatiotemporal distribution of radiocarbon determinations with the onset of key economic transitions. The region of study is here defined on the basis of climatic, geographical and cultural criteria (Iriarte et al., 2016). It encompasses the subtropical domains of the Paraguay, Paraná and Uruguay River Basins (which form the La Plata River) together with the adjacent Atlantic coast (Fig. 1). Most of the study area coincides with the La Plata Basin proper. However, because we considered cultural as well as geographical criteria in the delimitation of the study zone, areas that are not technically part of the basin are also included in the analysis. This is the case, for example, with the Uruguayan pampas, whose archaeology has deep connections to that of the subtropical areas of southern Brazil (Iriarte, 2006). Similarly, the southern Brazilian Atlantic coast was settled by cultures that were also widespread in the interior of the La Plata Basin (Bonomo et al., 2015; Noelli and Souza, 2017). In contrast, some areas that are technically part of the La Plata Basin are not addressed – such as the wetlands and savannas that form the basin’s headwaters – as they have cultural connections elsewhere (the Amazon, Central Brazil) or have insufficient radiocarbon data.

The study region is a privileged setting in lowland South America for evaluating the signal of the NDT in Neotropical contexts: unlike (most parts of) the Amazon, where the scarcity of dates reliably affiliated to

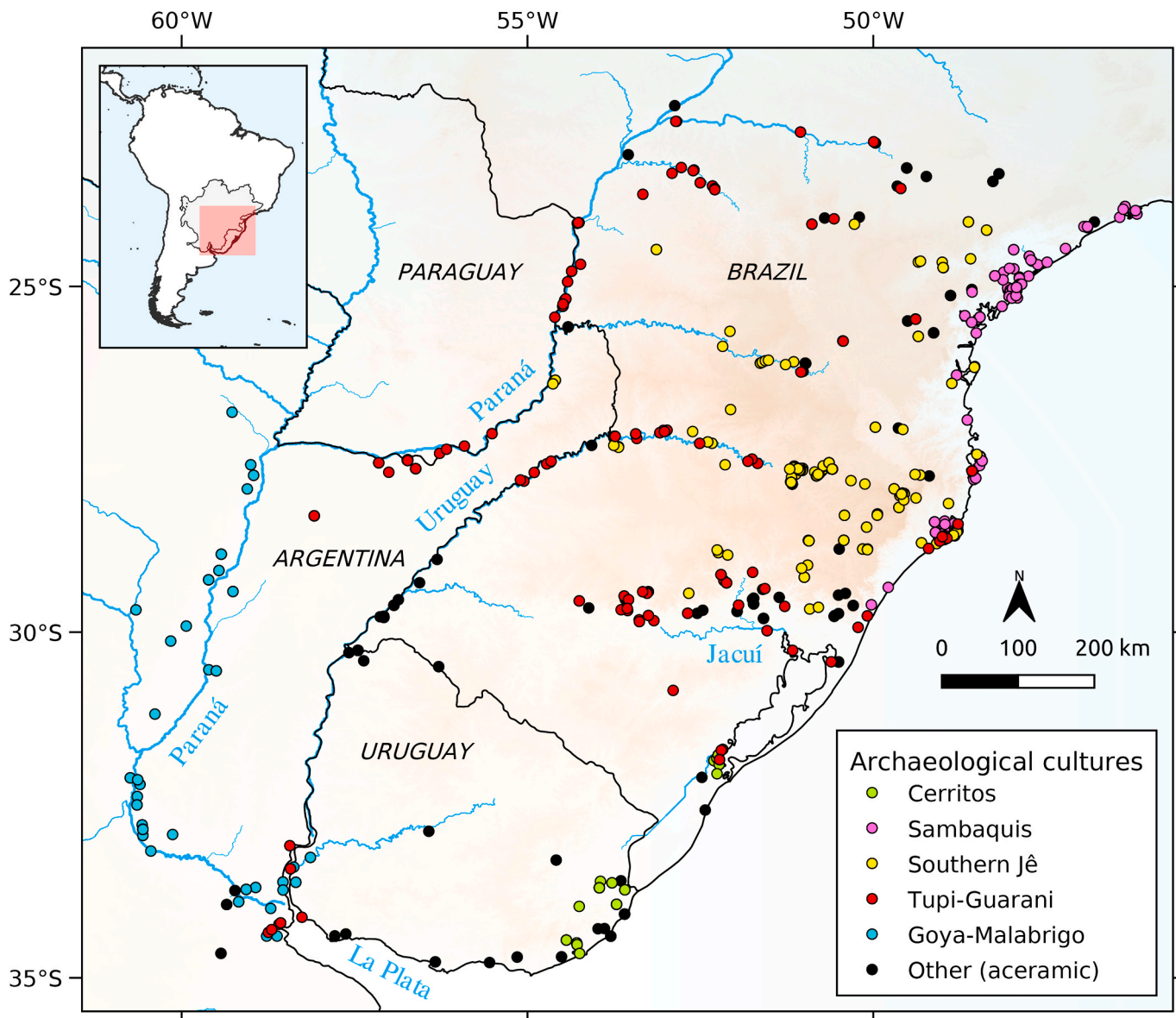


Fig. 1. Archaeological sites analysed in the paper. The limits of the La Plata Basin are shown in the inset.

distinct archaeological cultures undermines the significance of conclusions based on aggregated radiocarbon data (Riris, 2019), the ELBAC has a considerable density and coverage of high-quality data (Iriarte et al., 2016). Crucially, the introduction of plant cultivation to the region coincides, in part, with cultural dispersals from other parts of South America – namely, the Guarani from the Amazon Basin and the Jê from central Brazil (De Souza et al., 2020; Iriarte et al., 2016). Both traditions relied on agroforestry and the formation of anthropogenic forests (Noelli, 1998; Robinson et al., 2018). At the same time, before the arrival of the Guarani and southern Jê, cultivated plants were already present and may have played an important role in the development of the mid-Holocene societies of Uruguay and the Brazilian coast, who engaged in the construction of earthen and shell mounds (Iriarte et al., 2004; Wesolowski et al., 2010). Thus, both endogenous and exogenous processes were at play at different times in the transition to agroforestry-based economies in the ELBAC.

In this paper, we aim to address the following questions: does the demographic trajectory in the ELBAC repeat the “boom and bust” patterns that have been argued to follow the adoption of agriculture elsewhere (Timpson et al., 2014)? Or did the region experience lower

growth rates, due to a lower expansion capacity of polyculture agroforestry and to the lag between first adoption of domesticates and full reliance on plant cultivation in the tropics (Fausto and Neves, 2018)? Are there regional variations within the ELBAC?

In what follows, we briefly review the evidence for the adoption of cultivated plants in the major cultural traditions of the ELBAC, before moving to the analysis of the radiocarbon record. For a thorough review of the archaeology of the region, we refer the reader to Iriarte et al. (2016).

1.1. Evidence of plant cultivation in the ELBAC

The currently available archaeobotanical data suggest that the transition to plant cultivation in the ELBAC, similar to other cases in lowland South America, was multifocal, responding to endogenous and exogenous processes. In southeastern Uruguay, the earliest evidence of domesticated plants is provided by phytoliths of maize (*Zea mays*) and squash (*Cucurbita* sp.) from preceramic contexts of mound villages (Cerritos) ~4700 cal BP (Iriarte et al., 2004). The presence of maize and other cultigens, including beans (*Phaseolus* sp.), has been confirmed

from phytolith and starch grain evidence from Cerritos sites dated at least ~3900-2900 cal BP (Iriarte, 2003). In other sites that have been analysed, however, phytoliths of cultigens (maize and beans) appear only after ~2000 cal BP, suggesting some temporal heterogeneity in the adoption of plant cultivation or perhaps a late intensification of that strategy (del Puerto et al., 2016). The adoption of cultigens in the region coincides with transformations in site architecture and settlement patterns by Cerritos societies, with the appearance of more permanent sites and formal architectural layouts, including circular arrangements of mounds around central plazas (Iriarte et al., 2004).

In the southern Brazilian coast, starch grains recovered from dental calculi of individuals buried in shell mounds (Sambaquis) attest the consumption of sweet potato (*Ipomoea batatas*) and yam (*Dioscorea* sp.), among other cultigens, since ~4800 cal BP, thus showing the adoption of plant cultivation at approximately the same time as in the Uruguayan Cerritos (Wesolowski et al., 2010). The importance of tubers has been confirmed by stable isotope analysis and oral health markers, which attest the consumption of carbohydrate-rich plants among Sambaqui societies ~4800-4100 cal BP (Pezo-Lanfranco et al., 2020). Starch grains of maize appear in dental calculi after ~2900 cal BP, contemporary with the first evidence for squash in the form of carbonized seeds (Boyadjian et al., 2016; Scheel-Ybert and Boyadjian, 2020). Microbotanical evidence from dental calculi also attest the presence of maize after ~1300 cal BP, associated with the arrival of the southern Jê tradition to the coast (see below) (Wesolowski et al., 2010). The Brazilian Sambaquis represent an intensification of coastal adaptations during the mid-Holocene, long thought to reflect larger and more sedentary populations whose economy was based on marine resources, with the monumental shell mounds currently interpreted as ceremonial sites for collective burials around key points of the coastal landscape (De Blasis et al., 2007).

A second wave of transition comes with the arrival of cultural traditions from outside the ELBAC: the Guarani and the southern Jê. The Guarani represent the southernmost branch of the Tupi-Guarani family, which spread from either southwestern or (most likely) eastern Amazon to the Paraná basin, Atlantic coast, and most forested areas of eastern South America (Bonomo et al., 2015; Brochado, 1984; Iriarte et al., 2017; Noelli, 1998). Archaeologically, the northernmost parts of the ELBAC were also occupied by the Tupinambá, so that we use the more inclusive label "Tupi-Guarani" in Table S1. Guarani sites are distributed around major navigable rivers and forested areas of the ELBAC, recognized by distinct anthrosols, corrugated and polychrome ceramics and urn burials (Bonomo et al., 2015; Milheira and DeBlasis, 2014; Noelli, 1998). There is ample ethnohistorical evidence for the role of forest management and polyculture agroforestry among the Guarani and other Tupi-Guarani populations, who brought a rich package with many varieties of cultivated plants (maize, manioc, beans, sweet potato, among others) to the regions they settled (Noelli, 1993). In fact, pollen evidence of maize ~2000 cal BP in southern Brazil coincides with the approximate date of arrival of the Guarani to the region (Behling et al., 2005). Currently, direct evidence for the consumption of maize and beans by the Guarani is provided by starch grains recovered from ceramic sherds ~500 cal BP (Schneider et al., 2016).

The southern Jê, archaeologically identified as the Taquara/Itararé tradition, represent the southernmost branch of the Jê family that spread throughout the central Brazilian savannah (cerrado) and reached the southern Brazilian highlands and adjacent coast (Noelli, 2005; Noelli and Souza, 2017). Archaeological sites in the highlands incorporate earthen architecture, with pit houses, ceremonial enclosures and burial mounds (Corteletti and Iriarte, 2018; Noelli and Souza, 2017). After ~1000 cal BP, the highest density of sites is attained, coupled with evidence for emerging socio-political hierarchies in the settlement and funerary records (De Souza et al., 2016a, 2016b). The demographic trajectory of the southern Jê seems to have been sustained by an agroforestry base, combining plant cultivation and forest management, potentially influencing the spread and maintenance of *Araucaria*

angustifolia (Robinson et al., 2018). As in the Guarani case, the first appearance of maize pollen in southern Jê territory (in the highlands of Misiones, Argentina) is dated to ~1800 cal BP, broadly coinciding with the southern Jê arrival to the ELBAC (Gessert et al., 2011). Archaeobotanical data available so far indicate the presence of maize, squash, beans and manioc in domestic contexts ~600 cal BP (Corteletti et al., 2015). In ceremonial contexts, ceramics from a large mound and enclosure complex yielded phytoliths of maize in a context related to ceremonial feasting dated ~700 cal BP (Iriarte et al., 2008). Preserved maize cobs were recovered from a funerary rock shelter of similar age (Lazzarotto et al., 1971). As mentioned above, on the coast, southern Jê burials dated ~1300 cal BP, postdating the Sambaquis, contained starch grains of sweet potato and maize in their dental calculi (Wesolowski et al., 2010).

Finally, in the lower Paraná, the local Goya-Malabrigo tradition has also been considered a dispersal from Amazonian environments, potentially related to Arawak speakers based on ceramic decoration, settlement patterns and social organization as described in historical accounts (Politis and Bonomo, 2012). That association, however, has been questioned by proponents of a local origin for the ceramic complex (Loponte and Acosta, 2016). Whatever the case, the Goya-Malabrigo occupied settlements with mounded architecture along the floodplains of the lower Paraná and its delta beginning around 2000 cal BP (Bonomo et al., 2011b). Evidence for plant cultivation in the region spans almost the entire duration of the Goya-Malabrigo tradition. Maize starch is attested since ~1650 cal BP (Bonomo et al., 2017), whereas phytoliths and starch grains of beans, maize and manioc were recovered from ceramic sherds and stone artefacts in contexts dated ~1100-500 cal BP (Bonomo et al., 2011a, 2017).

In summary, currently available archaeobotanical data suggest two periods of incorporation of cultivated plants into local economies. The first, ~4800 cal BP, attested in the Cerritos and in the Sambaquis, appears to have resulted from an endogenous process that also involved increased sedentism and emergence of earthen and shell monumental architecture. The second, ~2000 cal BP, was promoted by the arrival of the Guarani and southern Jê to the ELBAC, bringing with them a package of domesticated plants and agroforestry practices from lower latitudes (Bonomo et al., 2015; Corteletti and Iriarte, 2018). The arrival of the Goya-Malabrigo tradition to, or potentially its local emergence in the ELBAC, was part of the same transition. Even though domesticated plants were already present among the Cerritos and Sambaquis, the second wave brought plant cultivation to areas where it was previously unattested, as in the case of the southern Brazilian highlands.

Based on the broad picture defined above, we proceed to analyse aggregated radiocarbon determinations in order to assess population dynamics in relation to the identified economic transitions in the ELBAC. Specifically, we aim to test the following hypotheses:

1. If ELBAC societies experienced demographic processes similar to those of Eurasia, it is expected that statistically significant peaks in the SPDs will follow the appearance of plant cultivation;
2. Alternatively, if polyculture agroforestry as practised in the tropics provided a lower expansion capacity than Eurasian agriculture (Harris, 2002), no significant peaks should be observed.

The multifocal, diffuse nature of the adoption of cultivated plants in the ELBAC, as in other parts of South America (Piperno, 2011), offers a further challenge. Different responses may have been triggered by the two proposed transitions (~4800 and ~2000 cal BP):

3. It is possible that a double boom-and-burst pattern will be observed following each of the transitions;
4. Alternatively, a slow transition could be followed by a dramatic increase in the second moment, if the latter incorporated other elements (beyond plant cultivation) that fostered population growth (Kohler and Reese, 2014). This scenario is expected under the

hypothesis of a long delay, in the Neotropics, between first adoption of crops and a heavier dependence on cultivation (Fausto and Neves, 2018).

2. Materials and methods

2.1. Compilation of radiocarbon dates

We compiled a total of 1139 radiocarbon dates from 504 archaeological sites in the ELBAC. Dates and site coordinates were compiled from a variety of sources, including published literature, unpublished reports and existing databases (Bonomo et al., 2015; De Blasis et al., 2007; Noelli, 1999; Noelli and Souza, 2017; Politis and Bonomo, 2012), which were cross-checked with the original sources (Table S1). Although we are principally interested in mid- and late Holocene economic transitions, we compiled dates available for all periods since the late Pleistocene. The analysis was limited to the period 6000-500 cal BP, which encompasses the duration of the archaeological cultures of interest and allows us to observe the trends that precede the first occurrence of plant domesticates ~4800 cal BP. Extending the time window to ca. a millennium before the economic transition of interest is a procedure previously adopted in the analysis of SPDs as a paleodemography proxy (Shennan et al., 2013). As per standard practise, however, models are fitted including dates within 500 years of the time window so as to avoid edge effects. The selected time window also dovetails with the transition in South American palaeodemographic dynamics suggested by (Goldberg et al., 2016). Our period of interest ends at the approximate date of the Columbian encounter, since later demographic processes cannot be dissociated from the impact of that event.

2.2. SPDs

Analysis was performed with the rcarbon 1.3.3 package for R (R Core Team, 2018).

For the SPDs, dates were calibrated using the ShCal20 curve (Hogg et al., 2020), except for those obtained on marine shell, in which cases we used the Marine20 curve (Heaton et al., 2020) and average ΔR offsets and errors based on the 10 nearest published values (<http://calib.org/marine/>). To account for oversampling of some sites, we aggregated dates from the same site into 200-year bins. SPDs are not normalised in order to minimize artefacts of the calibration curve on their shapes (Bevan et al., 2017).

2.3. Model testing

When comparing SPDs against a null hypothesis, an exponential model is commonly chosen, as it is assumed to reflect population growth in combination with taphonomic processes (Timpson et al., 2014). In addition to testing the observed SPD against a simple exponential model, we follow the established procedure of fitting multi-phase models with the aim of identifying changes in the demographic regime itself (Goldberg et al., 2016; Riris and Arroyo-Kalin, 2019). We accomplish this by fitting a suite of nine additional models (Models A to I) to the summed

calibrated probability distributions for the ELBAC, representing different potential demographic models and points of transition between them. Our range of models is based on qualitative inspection of the shape of the SPD. We formally compare the fits with Akaike's Information Criterion (AIC) (Table 1) to penalize model complexity while optimizing information gain, following precedent in the literature (Fernández-López de Pablo et al., 2019; Riris and Arroyo-Kalin, 2019). To do so, we extracted model likelihoods for each fitted model, calculated AICs, and summed them to derive overall model weights and ΔAIC values. As likelihoods are additive, so is the AIC (Burnham and Anderson, 2002, 2004).

To assess the goodness-of-fit of these models, simulated SPDs are produced by generating a number of random dates (equivalent to the number of bins in the empirical dataset) based on the assumed distribution (e.g. exponential), for a number of Monte Carlo runs ($n = 999$). A 95% confidence interval is then calculated from the simulated SPDs, and significant deviations from the null model are highlighted by comparing the empirical SPD to that envelope.

2.4. Permutation tests

To assess regional departures from the global demographic trajectory in the ELBAC, we employed a random mark permutation test (Crema et al., 2016). In this procedure, the marks (in this case, regional affiliation) associated with each bin are randomly shuffled, and simulated SPDs are computed for a number of Monte Carlo runs ($n = 999$). The simulated SPDs are then used to calculate a 95% confidence interval that represents the null of no spatial structure in the subsets of the empirical data. Significant regional departures from the global SPD are defined as the periods where the empirical SPDs are above or below that envelope. For the marks, we subdivided our dataset into four regions of cultural and geographical pertinence:

Region 1: the Atlantic coast, whose sites are mostly related to the Sambaqui societies.

Region 2: the pampas or plains of Uruguay and adjacent southern Brazil, broadly coinciding with the extent of the Cerritos;

Region 3: the southern Brazilian highlands, primarily occupied by the southern Jê;

Region 4: the forested lowlands of the middle Paraná, Uruguay, Jacuí Rivers and neighboring areas settled by the Guarani;

Region 5: the lower Paraná and its delta, mainly occupied by the Goya-Malabrigo tradition.

Although each region has the predominance of a particular archaeological tradition, the analysis has been carried out considering all sites independently of cultural affiliation. Besides the fact that cultural affiliations are not always agreed upon, subdividing the data could mask the broad demographic patterns in a region for a given time period. Including all dates is justified by previous studies concerning regional population changes relative to economic transitions (Shennan et al., 2013).

In addition to comparing each local SPD to the pan-regional trend, we performed pairwise comparisons of the permutation test of all regions (Fig. S2). All of the procedures described in this section are

Table 1

Comparison of statistical fits to the empirical SPD for the ELBAC study region.

Model	Type	Breakpoint (cal BP)	Parameters	Total AIC	ΔAIC	w
I	Exponential, Linear, Exponential	4000, 2000	3, 3, 3	-104665	0	1
H	Exponential, Linear, Exponential	4000, 1500	3, 3, 3	-104635	30.9	1.89E-07
G	Logistic, Linear, Exponential	4000, 2000	5, 3, 3	-104105	560.8	1.61E-122
F	Linear, Linear, Linear	4000, 1500	3, 3, 3	-104072	593.5	1.29E-129
C	Logistic & Exponential	2000	5, 3	-100837	3828.9	0
E	Logistic & Exponential	3000	5, 3	-99391	5274.5	0
D	Logistic & Logistic	4000	5, 5	-95134	9531.8	0
A	Exponential	N/A	3	-88605	16060.7	0
B	Logistic	N/A	5	-87874	16791.6	0

available as R code in the supplementary information (Appendix S3).

3. Results and discussion

3.1. Model-fitting

The observed SPD for all sites in the ELBAC significantly departs from a null exponential model for the period of interest (Fig. 2a). Two positive deviations are observed at ~5400–3900 and ~800–500 cal BP, intercalated with a period of negative deviation ~2800–1300. Having confirmed the inadequacy of an exponential model to explain the ELBAC data we found that the best-fit model (Model I) adequately describes the observed SPD by combining a phase of exponential growth ~6000–4000 cal BP, followed by a gently linear decrease ~4000–2000 cal BP and, finally, a renewed phase of exponential growth ~2000–500 cal BP (Fig. 2B, Fig. S4, Table 1). The first part of the overall trend is in agreement with previous models published for the entire South American continent, which show exponential growth following ~6000–5500 cal BP (Goldberg et al., 2016; Riris and Arroyo-Kalin, 2019). The putative early Late Holocene phase of population contraction, as opposed to stabilisation at theoretical carrying capacity (Goldberg et al., 2016), is, to the best of our knowledge, unique to the ELBAC.

3.2. Permutation test

Demographic trends were not homogeneous throughout the research area. The results of the permutation test show that all regional SPDs exhibited significant departures from the pan-regional trend (Fig. 3). Overall, trajectories are asynchronous and in antiphase between two broad regions: (1) the coast and the pampas, and (2) the southern Brazilian highlands, Paraná lowlands and delta. Whereas the former regions show positive deviations until ~2000 cal BP, followed by decline, the latter show negative deviations until ~2000 cal BP, followed by growth. The pairwise permutation test reinforces this result, with the SPDs for the coast and pampas showing no statistically significant deviations from each other, but exhibiting significant deviations from the other three regions (Fig. S2). It is important to notice that the latter also show some regional variation, since only the permutation of the lower Paraná and the southern Brazilian highlands exhibited non-significant results (Fig. S2).

Comparing the regional curves with the best-fit model for the entire ELBAC, we may conclude that the three-phase model can be attributed to higher activity (albeit under different demographic regimes) in the coast, in the first instance (exponential growth ~6000–4000 cal BP), and in the highlands and Paraná delta, in a second moment (exponential growth ~2000–500 cal BP).

The pattern evidenced in the permutation test mimics the spatio-temporal heterogeneity in the adoption of plant cultivation, which is earlier in the coast and pampas, but a causal relationship is not obvious. In the coast, a significant positive deviation from the pan-regional trend spans the entire period ~6000–2000 cal BP (Fig. 3a), a peak of activity which coincides with the flourishing of the Sambaquis and the first adoption of plant domesticates. The earliest available evidence for consumption of cultivated plants, however, postdates the onset of significant growth in the region (Wesolowski et al., 2010). Thus, rather than promoting unprecedented demographic growth, plant cultivation may have been incorporated in the economy of populations that were already relatively large, settled and densely distributed thanks to the exploitation of marine resources. Indeed, the distinctiveness of social trajectories in coastal environments, whose abundant and predictable resources are capable of sustaining high population densities and sedentism, has long been recognized (Fitzpatrick, 2020). For example, it was recently shown that, contrary to many other regions of Europe, population growth in Scandinavia precedes the Neolithic, which has been attributed to the high productivity of marine environments during the Mesolithic (Lewis et al., 2020). In South America, the most obvious example is the emergence of sedentism and social complexity along the Pacific Coast of Chile and Peru ~7000–4000 cal BP during a phase of increased freshwater availability and high marine productivity (Beresford-Jones et al., 2018; Marquet et al., 2012).

The positive deviation prior to the adoption of cultivars deserves some attention in light of optimal foraging models that propose population packing as a driver of domestication (Kennett and Winterhalder, 2006). For example, in the Mediterranean rim, pressure over high-ranked game and declines in hunting intensity throughout the Epipalaeolithic have been demonstrated through shifts in prey composition, suggesting that population pressure played a role in Late Holocene developments such as the transition to agropastoralism (Munro et al., 2018; Stiner et al., 1999). In Eastern North America, kernel density estimates (KDE) of taphonomically-corrected aggregated

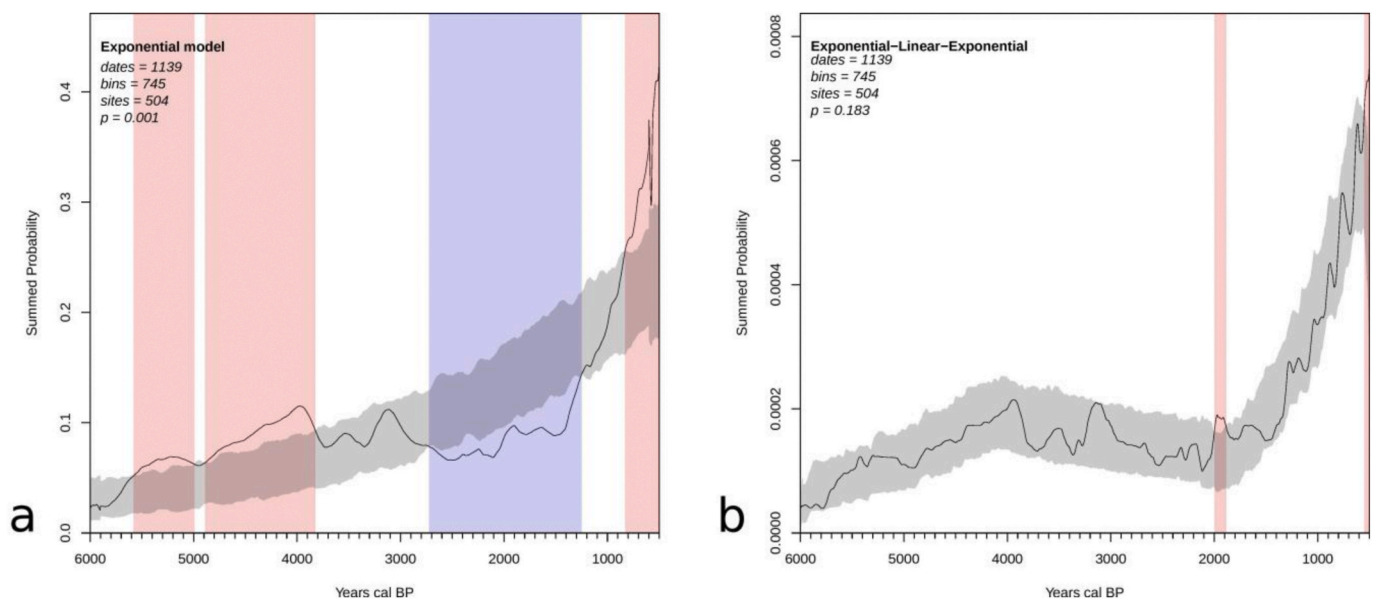


Fig. 2. a) Test of SPD against exponential null model. b) Best-fit demographic model (exponential-linear-exponential, with breakpoints at ~4000 and 2000 cal BP). The confidence interval from the simulated dataset is shaded in grey, and areas of significant positive and negative deviations are highlighted in red and blue, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

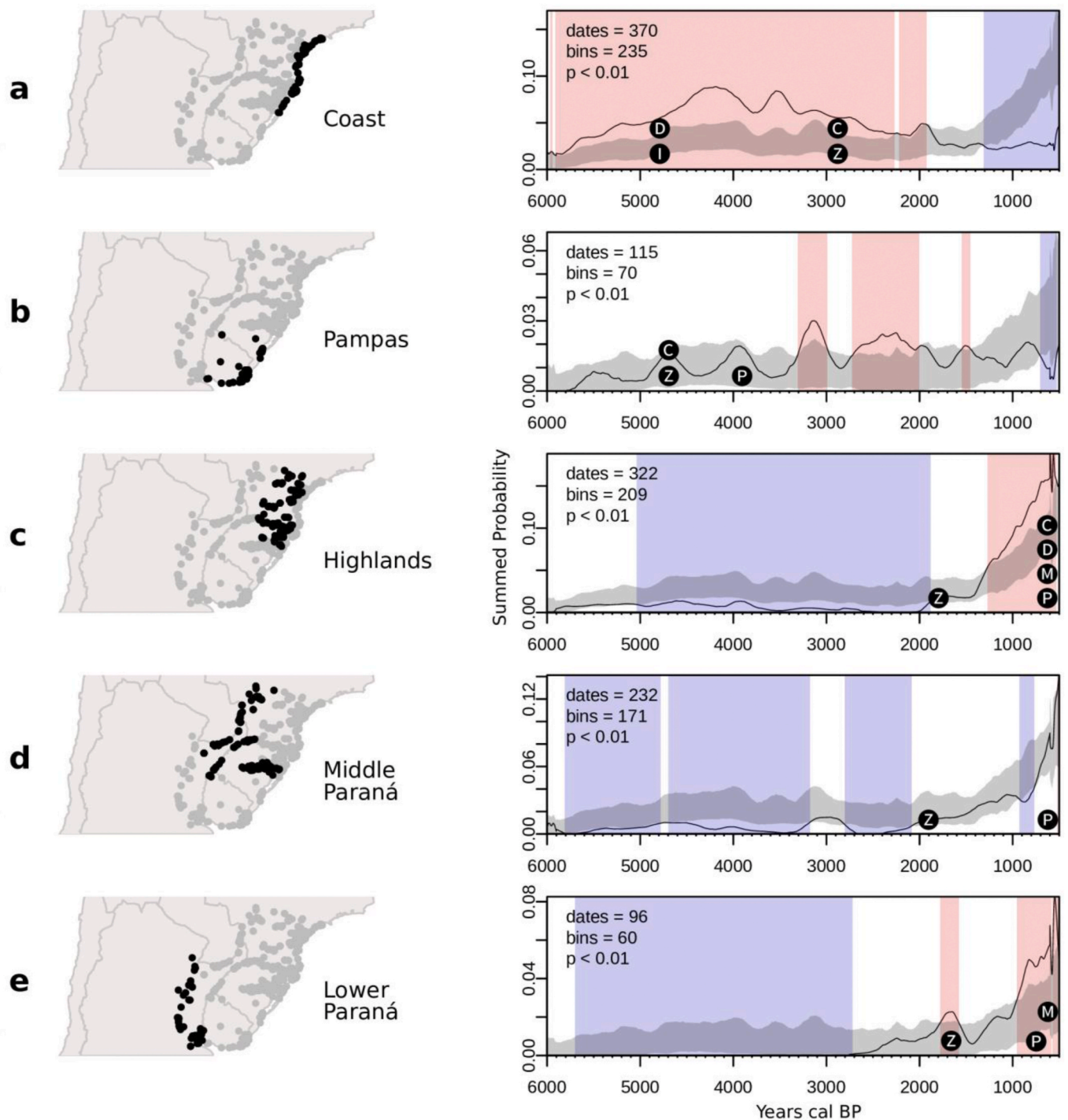


Fig. 3. Results of the permutation test. a) Atlantic coast; b) pampas; c) southern Brazilian highlands; d) Paraná, Uruguay and Jacuí lowlands; e) lower Paraná and its delta. The confidence envelope obtained for each simulated dataset is shaded in grey, and the areas of significant positive (red) and negative (blue) deviation are highlighted. The earliest evidence of the most important plant domesticates in each region is indicated by the following letters: C = *Cucurbita* sp. (squash), D = *Dioscorea* sp. (yam), I = *Ipomoea batatas* (sweet potato), M = *Manihot esculenta* (manioc), P = *Phaseolus* sp. (beans), Z = *Zea mays* (maize). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

radiocarbon data also point to large Mid Holocene populations prior to the adoption of domesticates (Weitzel and Coddling, 2020). In the ELBAC, however, the same pattern cannot be inferred solely from the radiocarbon record of other regions except for the coast.

In summary, the early activity among the Sambaquis appears to drive the first phase of demographic regime in the ELBAC (exponential growth ~6000-4000 cal BP), a period when other regions (the southern highlands, Paraná lowlands and delta) exhibit long negative deviations from

the pan-regional trend (Fig. 3). Although the first adoption of cultivated plants in the ELBAC occurred during this period, a causal relationship with population growth in the coast cannot be established, and a negative deviation from the pan-regional trend is evident in the coast after ~1300 cal BP, even though plant cultivation had been part of local economies for millennia (Fig. 3a). We caution against over-interpreting sustained negative deviations in the permutation test over the early exponential growth phase, as low archaeological visibility and low

sampling intensity may also be affecting inland and riverine occupations during this period, in contrast to the impressive Sambaqui sites (e.g. Gilson and Lessa, 2020).

The situation of the pampas is not as clear, with peaks of positive deviation from the negative, linear pan-regional trend ~4000-1500 cal BP (Fig. 3b). Local growth, however, may be unrelated to changes in the subsistence system. The first significant deviation follows, by several centuries, the earliest evidence of domesticated plants among the Cerritos (Iriarte et al., 2004). The bulk of the positive local deviations seen in the pampas after ~3300 cal BP (Fig. 3b) coincides with the transformation of Cerritos societies through the arrival of ceramics, diversification of mound architecture and greater formalization of village plans (Iriarte, 2003). Thus, we suggest that socio-political factors may have been more decisive in shaping the demographic trajectory of the region than the adoption of cultivated plants by itself. Alternatively, it is possible that the observed peaks are related to a later adoption (or intensification) of plant cultivation among most Cerritos societies, as in the case of the sites analysed by del Puerto et al. (2016), where crops only appear after ~2000 cal BP. Similar to the coast, sustained growth is apparently never achieved, with a noticeable decline in the final part of the sequence (Fig. 3b).

In the southern Brazilian highlands, the arrival of the southern Jê, coinciding with the first evidence of maize (Gessert et al., 2011), is followed by a positive deviation from the pan-regional trend after ~1300 cal BP, in antiphase with the coast (Fig. 3c). Although the arrival of the southern Jê coincides with the onset of the second phase of exponential growth in the best-fit model for the whole ELBAC (~2000 cal BP), the deviation seen in the permutation test shows a delay of several centuries from the earliest date of that archaeological tradition. The period of local positive deviation coincides with two later phenomena: the expansion of *Araucaria* forests, potentially due to anthropogenic influence (Bitencourt and Krauspenhar, 2006; Iriarte and Behling, 2007; Robinson et al., 2018), and the development of novel forms of ceremonial and domestic architecture reflecting the formalization of leadership and growing inequality in the highlands (De Souza, 2018; De Souza et al., 2016a; Iriarte et al., 2008).

At the same time, the forested lowlands settled by the Guarani after ~2000 cal BP do not show a significant deviation from the pan-regional demographic trend, which is exponential at this point (Fig. 3d). Before that time period, the region shows the same long negative deviation as the highlands and Paraná delta, in contrast with the trend observed in the coast and pampas. A rapid demographic expansion – or “swarming” – has long been accepted as the main process of Guarani spread (Bonomo et al., 2015; Brochado, 1984; Noelli, 1998). This would lead us to expect a significant positive deviation from the pan-regional trend in the areas occupied by that archaeological culture after ~2000 cal BP. The absence of such trend is intriguing and adds to the results of recent simulation-based approaches that failed to replicate the Guarani expansion as a purely demographic dispersal – but the presence of questionable dates, lack of spatial structure in their distribution and overall incompleteness of the radiocarbon record must also be taken into account (De Souza et al., 2020).

We suggest that the principal driver of exponential population growth in the period following ~2000 cal BP in the ELBAC was triggered by the arrival of cultural traditions that originated outside the region: namely the southern Jê and Guarani, who introduced a diverse package of cultivated plants and active forest management in the region (Bonomo et al., 2015; Robinson et al., 2018), but also the Goya-Malabrigo. Even though current archaeobotanical evidence suggests plant domesticates were present much earlier, it was only with this second wave that a demographic signal comparable to the NDT is evident in the ELBAC.

The observed trend is in agreement with dietary reconstructions based on stable isotopes from human bone collagen. For the Sambaquis, data spanning from ~6700 to 1700 cal BP show a predominantly marine diet, except for inland populations with higher intake of C3 terrestrial

animals (Colonese et al., 2014). There is, however, evidence for a higher intake of C3 plants among some coastal groups ~4800-4100 cal BP and in later southern Jê sites, which also relied more heavily on terrestrial mammals (Pezo-Lanfranco et al., 2020). As for the Cerritos, although maize is present in the archaeobotanical record from early on, bone collagen $\delta^{13}C$ values are very depleted, with a single exception, even in samples dated later than ~2500 cal BP (Bracco et al., 2000; del Puerto et al., 2014). The same is true of Goya-Malabrigo human remains, which exhibit average $\delta^{13}C$ values lower than -19‰ from ~1600 cal BP to the contact and no significant changes over time, with only two samples suggesting a higher C4 intake (Bonomo et al., 2017; Ottalagano and Loponte, 2017). Among the archaeological traditions of the ELBAC, the southern Jê and Guarani exhibit the most enriched bone collagen $\delta^{13}C$ values, with some individuals reaching almost -10‰, but also much internal variation (Bonomo et al., 2017; De Masi, 2009; Loponte et al., 2016). Overall, the Guarani show values around -16 to -15‰, with the southern Jê yielding more depleted values, especially in the case of samples from the highlands. The absence of a strong C4 signal before the Guarani and southern Jê, even though maize is present in the archaeobotanical record, suggests maize may have been consumed in low quantities so as to be undetected isotopically for a long period of time until becoming a staple (Bonomo et al., 2017). Similarly, it is possible that C3 crops were more important than maize, as appears to be the case among some Sambaquis (Pezo-Lanfranco et al., 2020).

The palaeodemographic trajectory observed in our study area is different from that reconstructed for the South/Central Andes, Northwest Patagonia and South Patagonia by Perez et al. (2017) using mtDNA and frequencies of calibrated radiocarbon dates. In the South/Central Andes and Northwest Patagonia, abrupt population increases were noticed following the appearance of domesticated plants and animals. Furthermore, the region with the earliest time of adoption and diversity of cultivars (South/Central Andes, ~8500 cal BP) was shown to have attained the largest population. Although transition to marine diets was apparently also a driver of population growth, Perez et al. (2017) found that it was not sufficient to explain the difference between Northwest and South Patagonia: by ~2000 cal BP, the former had attained a population nearly twice the size of the latter, where domesticated resources were never adopted. In the ELBAC, in contrast, neither marine adaptations nor the age of adoption of cultivars were determinants of a region's sustained growth – as can be seen in the case of the coast and pampas, which never exhibited the steep increase seen in the highlands or Paraná delta (Fig. 3).

The delay attested in the ELBAC between first appearance of cultivars, population growth and isotopic evidence of agricultural diets should come as no surprise. A delay of over two millennia between the adoption of cultivated plants and significant population growth had been described elsewhere in the Americas (Kohler et al., 2008; Smith, 2015). A similar situation has been hypothesized for the areas closer to the centre of domestication in Eurasia. In the Levant, a lag of over one millennium has been documented between the first evidence of agriculture and considerable population growth, which is related to the emergence of large sedentary villages (Kuijt, 2008). Unlike Europe, where the spread of agriculture was a process driven, in large part, by migration, the areas where plant domestication was actually carried out may have experienced slower transitions. The same phenomenon has been postulated for North America (Bocquet-Appel and Naji, 2006).

Although it is tempting to see the demographic consequences of plant cultivation as dependent on whether domestication was carried out locally (slow transition) or brought by waves of migrant farmers (fast growth), the parallel with the ELBAC is imperfect. Cultivated plants like maize and sweet potato, which are present in the region by ~4800-4700 cal BP, were certainly not domesticated locally. Perhaps the fact that even the earliest crops introduced to the ELBAC were domesticated elsewhere is one of the causes of the lag between the first adoption of domesticates and significant population growth, as a pause might have been necessary before the adaptation of predominantly tropical plants to

the subtropical and temperate environments of the ELBAC (for a similar argument in North America and Austronesia, see Kohler et al., 2008; Spriggs, 2011).

4. Conclusion

The nature of food-producing economies in the Neotropics continues to be debated. At the same time that some parts of lowland South America show evidence of large-scale landscape transformations, it is argued that a pattern of plant cultivation without full reliance on agriculture was predominant in most of the region, and that a Neolithic-like economic transition was never truly achieved (Fausto and Neves, 2018). If that is indeed the case for most of the tropics of South America, it is expected that the demographic trajectories of the continent should also differ from the well-known patterns of ‘boom and bust’ following adoption of agriculture as seen, for example, in Europe (Shennan et al., 2013). For a deeper understanding of the question, we believe as many lines of evidence as possible should be examined. In addition, considering the diverse environments and human land use practises attested across lowland South America, more regional studies are necessary.

In this paper, we aimed to contribute to the debate by incorporating a further line of evidence – statistical analysis of aggregated radiocarbon measurements – in the eastern La Plata Basin and Atlantic Coast (ELBAC). We compared the patterns observed in the spatio-temporal distribution of radiocarbon dates with archaeobotanical evidence for the first appearance of domesticated plants. Our results confirm that, as in other parts of the American continent, a delayed transition is observed between the initial adoption of crops and sustained population growth. We further demonstrate that, in the ELBAC, demographic trends are asynchronous and often antiphased between different subregions. For example, whereas the Atlantic coast experiences a significant positive deviation ~6000-2000 cal BP, the same period is marked by a negative deviation in the southern Brazilian highlands, where significant growth occurs only after ~1300 cal BP. When considering the ELBAC as a whole, the spatially heterogeneous demographic trajectories are reflected in two phases of exponential growth (~6000–4000 and ~2000–500 cal BP) intercalated by a period of contraction. Current archaeobotanical evidence confirms that plant domesticates are introduced in the ELBAC ~4800-4700 cal BP, when the first trend of exponential growth in the SPDs is already established. Therefore, the adoption of plant cultivation appears to follow rather than cause population growth during that first period. It is only after ~2000 cal BP, with the arrival of new archaeological traditions – and their respective packages of crops, agroforestry practises and potential adaptations to subtropical environments – to the ELBAC that a causal relationship may be established between a higher reliance on domesticated plants and significant population growth. In summary, our results conform to the expectations of a hypothetical long delay between adoption of crops and the consequences of heavier economic reliance on food production (including the purported demographic transition) in the Neotropics. At the same time, however, we suggest that a signal compatible with the Neolithic demographic transition may be observed in lowland South America under certain conditions, as seen in the later part of our sequence. The precise conditions responsible for this relatively late regime shift is in need of further study.

As more radiocarbon data are obtained for other parts of lowland South America, and as archaeobotanical evidence comes into sharper focus, we expect that similar regional studies will shed further light on the complex relationships between shifts in subsistence and demographic regimes across the continent.

Declaration of competing interest

The authors declare no competing interests.

acknowledgment

JGS is funded by a Marie Skłodowska-Curie Individual Fellowship, project 840163, European Commission Horizon 2020.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2020.105293>.

References

- Arroyo-Kalin, M., Riris, P., 2020. Did pre-Columbian populations of the Amazonian biome reach carrying capacity during the Late Holocene? *Phil. Trans. R. Soc. B* 376, 20190715. <https://doi.org/10.1098/rstb.2019.0715>.
- Behling, H., Pillar, V.D., Bauermann, S.G., 2005. Late Quaternary grassland (Campos), gallery forest, fire and climate dynamics, studied by pollen, charcoal and multivariate analysis of the São Francisco de Assis core in western Rio Grande do Sul (southern Brazil). *Rev. Palaeobot. Palynol.* 133, 235–248.
- Beresford-Jones, D., Pullen, A., Chauca, G., Cadwallader, L., García, M., Salvatierra, I., Whaley, O., Vásquez, V., Arce, S., Lane, K., French, C., 2018. Refining the maritime foundations of andean civilization: how plant fiber technology drove social complexity during the preceramic period. *J. Archaeol. Method Theor* 25, 393–425. <https://doi.org/10.1007/s10816-017-9341-3>.
- Bettinger, R.L., 2016. Prehistoric hunter-gatherer population growth rates rival those of agriculturalists. *Proc. Natl. Acad. Sci. Unit. States Am.* 113, 812–814. <https://doi.org/10.1073/pnas.1523806113>.
- Bevan, A., Colledge, S., Fuller, D., Fyfe, R., Shennan, S., Stevens, C., 2017. Holocene fluctuations in human population demonstrate repeated links to food production and climate. *Proc. Natl. Acad. Sci. Unit. States Am.* 114, E10524–E10531. <https://doi.org/10.1073/pnas.1709190114>.
- Bitencourt, A.L.V., Krauspenhar, P.M., 2006. Possible prehistoric anthropogenic effect on *Araucaria angustifolia* (Bert.) O. Kuntze expansion during the Late Holocene. *Rev. Bras. Palaontol.* 9, 109–116.
- Blatrix, R., Roux, B., Béarez, P., Prestes-Carneiro, G., Amaya, M., Aramayo, J.L., Rodrigues, L., Lombardo, U., Iriarte, J., de Souza, J.G., Robinson, M., Bernard, C., Pouilly, M., Durécu, M., Huchzermeyer, C.F., Kalebe, M., Ovando, A., McKey, D., 2018. The unique functioning of a pre-Columbian Amazonian floodplain fishery. *Sci. Rep.* 8, 5998. <https://doi.org/10.1038/s41598-018-24454-4>.
- Bocquet-Appel, J.-P., 2011. When the world's population took off: the springboard of the Neolithic Demographic Transition. *Science* 333, 560–561.
- Bocquet-Appel, J., 2002. Paleoanthropological traces of a neolithic demographic transition. *Curr. Anthropol.* 43, 637–650.
- Bocquet-Appel, J., Naji, S., 2006. Testing the hypothesis of a worldwide neolithic demographic transition: corroboration from American cemeteries. *Curr. Anthropol.* 47, 341–365. <https://doi.org/10.1086/498948>.
- Bocquet-Appel, J.P., Bar-Yosef, O., 2008. The Neolithic Demographic Transition and its Consequences.
- Bonomo, M., Aceituno, F.J., Politis, G.G., Pochettino, M.L., 2011a. Pre-Hispanic horticulture in the Paraná Delta (Argentina): archaeological and historical evidence. *World Archaeol.* 43, 554–575.
- Bonomo, M., Angrizani, R.C., Apollinaire, E., Noelli, F.S., 2015. A model for the Guaraní expansion in the La Plata Basin and littoral zone of southern Brazil. *Quat. Int.* 356, 54–73.
- Bonomo, M., Politis, G., Gianotti, C., 2011b. Montículos, jerarquía social y horticultura en las sociedades indígenas del delta del Río Paraná (Argentina). *Lat. Am. Antiq.* 22, 297–333.
- Bonomo, M., Scabuzzo, C., Politis, G.G., Zucol, A.F., 2017. Stable carbon and nitrogen isotope studies in the Paraná river delta (Argentina): an approach to prehispanic diets. *Lat. Am. Antiq.* 28, 105–126. <https://doi.org/10.1017/laq.2016.6>.
- Boserup, E., 1965. *The Conditions of Agricultural Growth: the Economics of Agrarian Change under Population Pressure*. Aldine Publishing Company, New York.
- Boydjian, C.H.C., Eggers, S., Reinhard, K.J., Scheel-Ybert, R., 2016. Dieta no Sambaqui Jabuticabeira-II (SC): consumo de plantas revelado por microvestígios provenientes de cálculo dentário. *Cadernos do LEPAARQ* 13, 131–161.
- Bracco, R., Freireiro, M., Panarello, H., Odino, R., Souto, B., 2000. Dieta, modos de produção de alimentos y complejidad. In: Durán, A., Bracco, R. (Eds.), *Arqueología de Las Tierras Bajas*. Ministerio de Educación y Cultura, Montevideo, pp. 227–248.
- Brochado, J.J.J.P., 1984. *An Ecological Model of the Spread of Pottery and Agriculture into Eastern South America*. University of Illinois, Urbana-Champaign.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Socio. Methods Res.* 33, 261–304.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Cavalli-Sforza, L.L., Menozzi, P., Piazza, A., 1994. *The History and Geography of Human Genes*. Princeton University Press, Princeton.
- Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G., Woods, W.I., 2015. The domestication of Amazonia before European conquest. *Proc. Biol. Sci.* 282, 20150813.
- Colonese, A.C., Collins, M., Lucquin, A., Eustace, M., Hancock, Y., de Almeida Rocha Ponzoni, R., Mora, A., Smith, C., DeBlasis, P., Figuti, L., Wesolowski, V., Plens, C.R., Eggers, S., de Farias, D.S.E., Gledhill, A., Craig, O.E., 2014. Long-term resilience of

- late Holocene coastal subsistence system in southeastern South America. *PLoS One* 9, e93854.
- Corteletti, R., Dickau, R., De Blasis, P.A.D., Iriarte, J., 2015. Revisiting the economy and mobility of southern proto-Jê (Taquara-Itararé) groups in southern Brazilian highlands: starch grain and phytoliths analyses from the Bonin site, Urubici, Brazil. *J. Archaeol. Sci.* 58, 46–61.
- Corteletti, R., Iriarte, J., 2018. Recent advances in the archaeology of the southern proto-Jê people. *Encyclopedia of Global Archaeology*, pp. 1–11. https://doi.org/10.1007/978-3-319-51726-1_3037-1.
- Crema, E.R., Habu, J., Kobayashi, K., Madella, M., 2016. Summed probability distribution of 14C dates suggests regional divergences in the population dynamics of the jomon period in eastern Japan. *PLoS One* 11, e0154809. <https://doi.org/10.1371/journal.pone.0154809>.
- De Blasis, P., Kneip, A., Scheel-Ybert, R., Giannini, P., Gaspar, M.D., 2007. Sambaquis e paisagem: dinâmica natural e arqueologia regional no litoral sul do Brasil. *Arqueologia Sudamericana/Arqueologia Sul-Americana* 3, 29–61.
- De Masi, M.A.N., 2009. Aplicações de isótopos estáveis de 18/16O, 13/12C e 15/14N em estudos de sazonalidade, mobilidade e dieta de populações pré-históricas no sul do Brasil. *Rev. Arqueol.* 22, 55–76.
- De Souza, J.G., 2018. Rethinking households, communities and status in the southern Brazilian highlands. *J. Anthropol. Archaeol.* 52, 44–58. <https://doi.org/10.1016/j.jaa.2018.08.006>.
- De Souza, J.G., Alcaina Mateos, J., Madella, M., 2020. Archaeological expansions in tropical South America during the late Holocene: assessing the role of demic diffusion. *PLoS One* 15, e0232367.
- De Souza, J.G., Corteletti, R., Robinson, M., Iriarte, J., 2016a. The genesis of monuments: resisting outsiders in the contested landscapes of southern Brazil. *J. Anthropol. Archaeol.* 41, 196–212. <https://doi.org/10.1016/j.jaa.2016.01.003>.
- De Souza, J.G., Robinson, M., Corteletti, R., Cárdenas, M.L., Wolf, S., Iriarte, J., Mayle, F., DeBlasis, P., 2016b. Understanding the chronology and occupation dynamics of oversized pit houses in the southern Brazilian highlands. *PLoS One* 11, e0158127.
- del Puerto, L., Bracco, R., Capdepon, I., Inda, H., 2014. Silicofitolitos e isótopos estáveis como indicadores de paleodieta en la prehistoria del este de Uruguay. *Micro Paleobotánica*. Universidad de la República, La Paloma.
- del Puerto, L., Capdepon, I., Inda, H., 2016. Paleobotánica y subsistencia de los constructores de Cerritos del Holoceno tardío en el Este del Uruguay: análisis fitolítico en sedimentos y artefactos arqueológicos. *Tessituras* 4, 117–160.
- Denham, T.P., Iriarte, J., Vrydaghs, L. (Eds.), 2007. *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. Routledge, New York.
- Fausto, C., Neves, E.G., 2018. Was there ever a neolithic in the Neotropics? Plant familiarisation and biodiversity in the Amazon. *Antiquity* 92, 1604–1618. <https://doi.org/10.15184/aqy.2018.157>.
- Fernández-López de Pablo, J., Gutiérrez-Roig, M., Gómez-Puche, M., McLaughlin, R., Silva, F., Lozano, S., 2019. Palaeodemographic modelling supports a population bottleneck during the Pleistocene-Holocene transition in Iberia. *Nat. Commun.* 10, 1872. <https://doi.org/10.1038/s41467-019-09833-3>.
- Fitzpatrick, S.M., 2020. Ancient aquaculture and the rise of social complexity. *Proc. Natl. Acad. Sci. Unit. States Am.* 117, 9151–9153. <https://doi.org/10.1073/pnas.2004254117>.
- Gayo, E.M., Latorre, C., Santoro, C.M., 2015. Timing of occupation and regional settlement patterns revealed by time-series analyses of an archaeological radiocarbon database for the South-Central Andes (16°–25°S). *Quat. Int.* 356, 4–14. <https://doi.org/10.1016/j.quaint.2014.09.076>.
- Gessert, S., Iriarte, J., Rios, R.C., Behling, H., 2011. Late Holocene vegetation and environmental dynamics of the Araucaria forest region in Misiones Province, NE Argentina. *Rev. Paleobot. Palynol.* 166, 29–37. <https://doi.org/10.1016/j.revpalbo.2011.04.006>.
- Gilson, S.-P., Lessa, A., 2020. Ocupação tardia do litoral norte e central catarinense por grupos pescadores-caçadores-coletores: uma revisão crítica do contexto cronológico dos sítios rasos com presença de cerâmica. *Rev. Arqueol.* 33, 55–77. <https://doi.org/10.24885/sab.v33i1.702>.
- Goldberg, A., Mychajliw, A.M., Hadly, E.A., 2016. Post-invasion demography of prehistoric humans in South America. *Nature* 532, 232. <https://doi.org/10.1038/nature17176>.
- Haak, W., Balanovsky, O., Sanchez, J.J., Koshel, S., Zaporozhchenko, V., Adler, C.J., Der Sarkissian, C.S.L., Brandt, G., Schwarz, C., Nicklisch, N., Dresely, V., Fritsch, B., Balanovska, E., Vilems, R., Meller, H., Alt, K.W., Cooper, A., the Genographic, C., 2010. Ancient DNA from European early neolithic farmers reveals their near eastern affinities. *PLoS Biol.* 8, e1000536. <https://doi.org/10.1371/journal.pbio.1000536>.
- Harris, D., 2002. The expansion capacity of early agricultural systems: a comparative perspective on the spread of agriculture. In: Bellwood, P., Renfrew, C. (Eds.), *Examining the Farming/language Dispersal Hypothesis*. McDonald Institute for Archaeological research, Cambridge, pp. 31–40.
- Heaton, T.J., Köhler, P., Butzin, M., Bard, E., Reimer, R.W., Austin, W.E.N., Bronk Ramsey, C., Grootes, P.M., Hughen, K.A., Kromer, B., Reimer, P.J., Adkins, J.F., Burke, A., Cook, M.S., Olsen, J., Skinner, L.C., 2020. Marine20 - the Marine Radiocarbon Age Calibration Curve (0 - 55,000 Cal BP), Simulated Data for IntCal20. <https://doi.org/10.1594/PANGAEA.914500>.
- Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S.M., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Bronk Ramsey, C., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L., 2020. SHCal20 SOUTHERN HEMISPHERE CALIBRATION, 0–55,000 YEARS CAL BP. *Radiocarbon*. <https://doi.org/10.1017/RDC.2020.59>, 1–20.
- Iriarte, J., 2009. Narrowing the gap: exploring the diversity of early food production economies in the Americas. *Curr. Anthropol.* 50, 677–680. <https://doi.org/10.1086/605493>.
- Iriarte, J., 2006. Landscape transformation, mounded villages, and adopted cultigens: the rise of early Formative communities in southeastern Uruguay. *World Archaeol.* 38, 644–663.
- Iriarte, J., 2003. Mid-Holocene Emergent Complexity and Landscape Transformation: the Social Construction of Early Formative Communities in Uruguay, La Plata Basin. University of Kentucky, Lexington.
- Iriarte, J., Behling, H., 2007. The expansion of Araucaria forest in the southern Brazilian highlands during the last 4000 years and its implications for the development of the Taquara/Itararé Tradition. *Environ. Archaeol.* 12, 115–127.
- Iriarte, J., DeBlasis, P., De Souza, J.G., Corteletti, R., 2016. Emergent complexity, changing landscapes, and spheres of interaction in southeastern South America during the middle and late Holocene. *J. Archaeol. Res.* <https://doi.org/10.1007/s10814-016-9100-0>.
- Iriarte, J., Elliott, S., Maezumi, S.Y., Alves, D., Gonda, R., Robinson, M., Gregorio de Souza, J., Watling, J., Handley, J., 2020. The origins of Amazonian landscapes: plant cultivation, domestication and the spread of food production in tropical South America. *Quat. Sci. Rev.* 248, 106582. <https://doi.org/10.1016/j.quascirev.2020.106582>.
- Iriarte, J., Gillam, J.C., Marozzi, O., 2008. Monumental burials and memorial feasting: an example from the southern Brazilian highlands. *Antiquity* 82, 947–961.
- Iriarte, J., Holst, I., Marozzi, O., Listopad, C., Alonso, E., Rinderknecht, A., Montaña, J., 2004. Evidence for cultivar adoption and emerging complexity during the Mid-Holocene in the La Plata Basin, Uruguay. *Nature* 432, 614–617.
- Iriarte, J., Power, M.J., Rostain, S., Mayle, F.E., Jones, H., Watling, J., Whitney, B.S., McKey, D.B., 2012. Fire-free land use in pre-1492 Amazonian savannas. *Proc. Natl. Acad. Sci. Unit. States Am.* 109, 6473–6478.
- Iriarte, J., Smith, R.J., Gregorio de Souza, J., Mayle, F.E., Whitney, B.S., Cárdenas, M.L., Singarayer, J., Carson, J.F., Roy, S., Valdes, P., 2017. Out of amazonia: late-holocene climate change and the tupi-guarani trans-continental expansion. *Holocene* 27, 967–975. <https://doi.org/10.1177/0959683616678461>.
- Kennett, D.J., Winterhalder, B. (Eds.), 2006. *Behavioral Ecology and the Transition to Agriculture*. University of California Press, Berkeley.
- Köhler, T.A., Glaude, M., 2008. The nature and timing of the Neolithic demographic transition in the North American Southwest. In: Bocquet-Appel, J.P., Bar-Yosef, O. (Eds.), *The Neolithic Demographic Transition and its Consequences*. Springer, New York, pp. 81–105.
- Köhler, T.A., Glaude, M.P., Bocquet-Appel, J.-P., Kemp, B.M., 2008. The Neolithic demographic transition in the US Southwest. *Am. Antiq.* 645–669.
- Köhler, T.A., Reese, K.M., 2014. Long and spatially variable Neolithic demographic transition in the North American Southwest. *Proc. Natl. Acad. Sci. Unit. States Am.* 111, 10101–10106.
- Kuijt, I., 2008. Demography and storage systems during the southern Levantine Neolithic demographic transition. In: Bocquet-Appel, J.P., Bar-Yosef, O. (Eds.), *The Neolithic Demographic Transition and its Consequences*. Springer, New York, pp. 287–313.
- Lazzarotto, D., Schmitz, P.I., Becker, I.B., Steinmetz, R., 1971. Pesquisas arqueológicas no Planalto. In: Duarte, P. (Ed.), *O Homem Antigo Na América*. Instituto de Pré-História, USP, São Paulo, pp. 79–89.
- Levis, C., Costa, F.R.C., Bongers, F., Peña-Claros, M., Clement, C.R., Junqueira, A.B., Neves, E.G., Tamañá, E.K., Figueiredo, F.O.G., Salomão, R.P., Castilho, C.V., Magnusson, W.E., Phillips, O.L., Guevara, J.E., Sabatier, D., Molino, J.-F., López, D.C., Mendoza, A.M., Pitman, N.C.A., Duque, A., Vargas, P.N., Zartman, C.E., Vasquez, R., Andrade, A., Camargo, J.L., Feldpausch, T.R., Laurance, S.G.W., Laurance, W.F., Killeen, T.J., Nascimento, H.E.M., Montero, J.C., Mostacedo, B., Amaral, I.L., Guimarães Vieira, I.C., Brienen, R., Castellanos, H., Terborgh, J., Carim, M., de, J.V., Guimarães, J.R., da, S., Coelho, L., de, S., Matos, F.D., de, A., Wittmann, F., Mogollón, H.F., Damasco, G., Dávila, N., García-Villacorta, R., Coronado, E.N.H., Emilio, T., Filho, D., de, A.L., Schietti, J., Souza, P., Targhetta, N., Comiskey, J.A., Marimon, B.S., Marimon, B.-H., Neill, D., Alonso, A., Arroyo, L., Carvalho, F.A., de Souza, F.C., Dallmeier, F., Pansonato, M.P., Duivenvoorden, J.F., Fine, P.V.A., Stevenson, P.R., Araujo-Murakami, A., Aymard, C.G.A., Baraloto, C., do Amaral, D.D., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Revilla, J.D.C., Stropp, J., Daly, D., Gribel, R., Paredes, M.R., Silveira, M., Thomas-Caesar, R., Baker, T.R., da Silva, N.F., Ferreira, L.V., Peres, C.A., Silman, M.R., Cerón, C., Valverde, F.C., Di Fiore, A., Jimenez, E.M., Mora, M.C.P., Toledo, M., Barbosa, E.M., Bonates, L.C., de, M., Arboleda, N.C., Farias, E., de, S., Fuentes, A., Guillaumet, J.-L., Jørgensen, P.M., Malhi, Y., de Andrade Miranda, I.P., Phillips, J.F., Prieto, A., Rudas, A., Ruschel, A.R., Silva, N., von Hildebrand, P., Vos, V.A., Zent, E.L., Zent, S., Cintra, B.B.L., Nascimento, M.T., Oliveira, A.A., Ramirez-Angulo, H., Ramos, J.F., Rivas, G., Schöngart, J., Sierra, R., Tirado, M., van der Heijden, G., Torre, E.V., Wang, O., Young, K.R., Baider, C., Cano, A., Farfan-Rios, W., Ferreira, C., Hoffman, B., Mendoza, C., Mesones, I., Torres-Lezama, A., Medina, M.N.U., van Andel, T.R., Villarreal, D., Zagt, R., Alexiades, M.N., Balslev, H., García-Cabrera, K., Gonzales, T., Hernandez, L., Huamantupa-Chuquimaco, I., Manzatto, A.G., Milliken, W., Cuenca, W.P., Pansini, S., Pauletto, D., Azevalo, F.R., Reis, N.F.C., Sampaio, A.F., Giraldo, L.E.U., Sandoval, E.H.V., Gamarra, L.V., Vela, C.I.A., ter Steege, H., 2017. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* 355, 925–931. <https://doi.org/10.1126/science.aal0157>.
- Lewis, J.P., Ryves, D.B., Rasmussen, P., Olsen, J., van der Sluis, L.G., Reimer, P.J., Knudsen, K.-L., McGowan, S., Anderson, N.J., Juggins, S., 2020. Marine resource abundance drove pre-agricultural population increase in Stone Age Scandinavia. *Nat. Commun.* 11, 2006. <https://doi.org/10.1038/s41467-020-15621-1>.
- Lombardo, U., 2010. Raised fields of northwestern Bolivia: a GIS based analysis. *Zeitschrift für Archäologie Außereuropäischer Kulturen* 3, 127–149.
- Loponte, D., Acosta, A., 2016. Los contextos Goya-Malabrigo del noreste argentino. *Cadernos do CEOM* 29, 125–187.

- Loponte, D., Carbonera, M., Corriale, M.J., Acosta, A., 2016. Horticulturists and oxygen ecozones in the tropical and subtropical forests of Southeast South America. *Environ. Archaeol.* 1–21. <https://doi.org/10.1080/14614103.2016.1211382>.
- Maezumi, S.Y., Alves, D.T., Robinson, M., De Souza, J.G., Levis, C., Barnett, R.L., Oliveira, E.A., Urrego, D., Schaan, D., Iriarte, J., 2018. The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nature Plants* 4, 540–547.
- Marquet, P.A., Santoro, C.M., Latorre, C., Standen, V.G., Abades, S.R., Rivadeneira, M.M., Arriaza, B., Hochberg, M.E., 2012. Emergence of social complexity among coastal hunter-gatherers in the Atacama Desert of northern Chile. *Proc. Natl. Acad. Sci. Unit. States Am.* 109, 14754–14760. <https://doi.org/10.1073/pnas.1116724109>.
- Milheira, R.G., DeBlasis, P., 2014. Tupi-guarani archaeology in Brazil. *Encyclopedia of Global Archaeology*. Springer, pp. 7384–7389.
- Munro, N.D., Bar-Oz, G., Meier, J.S., Sapir-Hen, L., Stiner, M.C., Yeshurun, R., 2018. The emergence of animal management in the southern levant. *Sci. Rep.* 8, 9279. <https://doi.org/10.1038/s41598-018-27647-z>.
- Neves, E.G., 2013. Was agriculture a key productive activity in pre-colonial amazonia? The stable productive basis for social equality in the central Amazon. In: Brondízio, E.S., Moran, E.F. (Eds.), *Human-Environment Interactions: Current and Future Directions*. Springer Netherlands, Dordrecht, pp. 371–388. https://doi.org/10.1007/978-94-007-4780-7_16.
- Neves, E.G., 2007. El Formativo que nunca terminó: la larga historia de la estabilidad en las ocupaciones humanas de la Amazonía Central. *Boletín de Arqueología* 11, 117–142.
- Noelli, F.S., 2005. Rethinking stereotypes and the history of research on Jê populations in South Brazil: an interdisciplinary point of view. In: Funari, P., Zarankin, A., Stovel, E. (Eds.), *Global Archaeological Theory. Contextual Voices and Contemporary Thoughts*. Springer, New York, pp. 167–190.
- Noelli, F.S., 1999. A ocupação humana na Região Sul do Brasil: arqueologia, debates e perspectivas-1872-2000. *Rev. Usp.* 44, 218–269.
- Noelli, F.S., 1998. The Tupi: explaining origin and expansions in terms of archaeology and of historical linguistics. *Antiquity* 72, 648–663.
- Noelli, F.S., 1993. Sem Tekohá não há Tekó: em busca de um modelo etnoarqueológico da subsistência e da aldeia Guarani aplicado a uma área de domínio no delta do Jacuí-RS. PUCRS, Porto Alegre.
- Noelli, F.S., Souza, J.G. de, 2017. Novas perspectivas para a cartografia arqueológica Jê no Brasil meridional. *Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas* 12, 57–84.
- Ottalagano, F., Loponte, D., 2017. Stable isotopes and diet in complex hunter-gatherers of Paraná River Basin, South America. *Archaeological and Anthropological Sciences* 9, 865–877. <https://doi.org/10.1007/s12520-015-0308-6>.
- Perez, S.I., Postillone, M.B., Rindel, D., 2017. Domestication and human demographic history in South America. *Am. J. Phys. Anthropol.* 163, 44–52. <https://doi.org/10.1002/ajpa.23176>.
- Pezo-Lanfranco, L., Eggers, S., Petronilho, C., Toso, A., da Rocha Bandeira, D., Von Tersch, M., dos Santos, A.M.P., Ramos da Costa, B., Meyer, R., Colonese, A.C., 2020. Middle Holocene plant cultivation on the atlantic forest coast of Brazil? *Royal Society Open Science* 5, 180432. <https://doi.org/10.1098/rsos.180432>.
- Piperno, D.R., 2011. The origins of plant cultivation and domestication in the New World tropics: patterns, process, and new developments. *Curr. Anthropol.* 52, S453–S470.
- Piperno, D.R., Pearsall, D.M., 1998. *The Origins of Agriculture in the Lowland Neotropics*. Academic Press, San Diego.
- Politis, G., Bonomo, M., 2012. La entidad arqueológica Goya-Malabrigo (ríos Paraná y Uruguay) y su filiación Arawak. *Rev. Arqueol.* 25, 10–46.
- Prates, L., Politis, G.G., Perez, S.I., 2020. Rapid radiation of humans in South America after the last glacial maximum: a radiocarbon-based study. *PLoS One* 15, e0236023.
- R Core Team, 2018. *R: A Language and Environment for Statistical Computing*.
- Rick, J.W., 1987. Dates as data: an examination of the Peruvian preceramic radiocarbon record. *Am. Antiq.* 55–73.
- Riris, P., 2019. Sparse radiocarbon data confound culture-climate links in late pre-columbian amazonia. *Quaternary*. <https://doi.org/10.3390/quat2040033>.
- Riris, P., 2018. Dates as data revisited: a statistical examination of the Peruvian preceramic radiocarbon record. *J. Archaeol. Sci.* 97, 67–76. <https://doi.org/10.1016/j.jas.2018.06.008>.
- Riris, P., Arroyo-Kalin, M., 2019. Widespread population decline in South America correlates with mid-Holocene climate change. *Sci. Rep.* 9, 6850. <https://doi.org/10.1038/s41598-019-43086-w>.
- Robinson, M., De Souza, J.G., Maezumi, S.Y., Cárdenas, M., Pessenda, L., Prufer, K., Corteletti, R., Scunderlick, D., Mayle, F.E., De Blasis, P., Iriarte, J., 2018. Uncoupling human and climate drivers of late Holocene vegetation change in southern Brazil. *Sci. Rep.* 8. <https://doi.org/10.1038/s41598-018-24429-5>.
- Scheel-Ybert, R., Boyadjian, C., 2020. Gardens on the coast: considerations on food production by Brazilian shellmound builders. *J. Anthropol. Archaeol.* 60, 101211. <https://doi.org/10.1016/j.jaa.2020.101211>.
- Schneider, F., Corteletti, R., Machado, N.T.G., Stülp, S., 2016. Arqueobotânica Guarani: a presença de Grãos de Amido, Fitólitos e Endocarpos Carbonizados no Sítio RS-T-114, Bacia do Rio Forqueta, Rio Grande Do Sul, Brasil. XIX Congresso de Arqueologia Argentina. Universidad Nacional de Tucumán, San Miguel de Tucumán, pp. 1001–1006.
- Shennan, S., Downey, S.S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., Manning, K., Thomas, M.G., 2013. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* 4.
- Shepard, G.H., Neves, E., Clement, C.R., Lima, H., Moraes, C., Santos, G.M. dos, 2020. *Ancient and Traditional Agriculture in South America: Tropical Lowlands*. Oxford Research Encyclopedia.
- Smith, B.D., 2015. A comparison of niche construction theory and diet breadth models as explanatory frameworks for the initial domestication of plants and animals. *J. Archaeol. Res.* 23, 215–262. <https://doi.org/10.1007/s10814-015-9081-4>.
- Spriggs, M., 2011. Archaeology and the Austronesian expansion: where are we now? *Antiquity* 85, 510–528. <https://doi.org/10.1017/S0003598X00067910>.
- Stiner, M.C., Munro, N.D., Surovell, T.A., Tchernov, E., Bar-Yosef, O., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283, 190–194. <https://doi.org/10.1126/science.283.5399.190>.
- Timpson, A., Colledge, S., Crema, E., Edinborough, K., Kerig, T., Manning, K., Thomas, M.G., Shennan, S., 2014. Reconstructing regional population fluctuations in the European Neolithic using radiocarbon dates: a new case-study using an improved method. *J. Archaeol. Sci.* 52, 549–557.
- Weitzel, E.M., Coddling, B.F., 2020. Population growth as a driver of initial domestication in Eastern North America, 3. *Royal Society Open Science*, p. 160319. <https://doi.org/10.1098/rsos.160319>.
- Wesolowski, V., Ferraz Mendonça de Souza, S.M., Reinhard, K.J., Ceccantini, G., 2010. Evaluating microfossil content of dental calculus from Brazilian sambaquis. *J. Archaeol. Sci.* 37, 1326–1338.