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# Long-Term Perspective on Fishing and Mammal Defaunation in the Atlantic Forest Coast of Brazil Using Archaeological Faunal Remains

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## Abstract

**Background and research aim:** Escalating anthropogenic threats to the Atlantic Forest, a renowned biodiversity hotspot, has placed the region in the spotlight for current conservation efforts. Faunal overexploitation and habitat degradation are among key factors driving the region's recent declines in faunal populations and biodiversity. Assessing the scale of these impacts is complicated by the near-complete absence of historical reference baselines. **Methodology:** Here, we provide a contribution to bridge this knowledge gap by analysing faunal remains from two historical archaeological sites, Morro Grande I (MG1) and Praia Grande Unidade 21 (PG-U21), in Babitonga Bay (Santa Catarina state, Brazil) dated between 1750 to 1950 AD. **Results:** Our results revealed that fishing and hunting played a crucial role in household consumption and economic livelihoods during the European colonisation of southern Brazil. Native terrestrial mammals made up a significant proportion of faunal remains at both sites. This suggests that species currently undergoing population declines were exploited in the region for at least the past two centuries. **Conclusion:** This study provides compelling evidence that the selective hunting of medium- and large-bodied native terrestrial mammals has persisted in the region for over 4500 years, and requires us to reconsider the idea of a heavy reliance on domestic animals during early European colonisation of southern Brazil. Our study thus traces the causes of regional terrestrial mammal defaunation back to the Pre-colonial and Historical times. **Implication for conservation:** We recommend the integration of historical and archaeological data into modern faunal population assessments and conservation initiatives to set more informed reference baselines.

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**Keywords**
Atlantic Forest, Babitonga Bay, faunal analysis, colonial fishing and hunting, mammal defaunation

## Introduction

Tropical and subtropical regions of South America are facing significant environmental and ecological challenges which parallel the global trends resulting from the rapid economic expansion of recent decades (Bogoni et al., 2020; Steffen et al., 2015; Verba et al., 2020). Brazil's renowned biodiversity hotspots of the Amazon and the Atlantic Forest (Colombo & Joly, 2010; Rezende et al., 2018) are currently undergoing rapid biodiversity and population loss due to overexploitation and habitat degradation (Ceballos et al., 2017; de Lima et al., 2020; Galetti et al., 2015, 2017; Scarano & Ceotto, 2015; Verba et al., 2020). Recent studies suggest a staggering loss of over 60% of mammals in the Atlantic Forest (Bogoni et al., 2020); unfortunately, such figures are likely an underestimation if reference baselines can be extended to include Pre-colonial and historical periods.

Studies have shown that certain anthropogenic stressors responsible for impacting animal diversity and abundance in recent decades have been present for over a century. As early as the mid-18th century, intellectual elites in colonial Brazil were already expressing increasing concern regarding the adverse environmental impacts of colonial economies, especially deforestation (Pádua, 2000). Similarly, in his seminal work the *Destruction of the Brazilian Atlantic Forest*, Dean discussed the persistent human impact on plants and animals in extensive regions of the Atlantic Forest since, at least, the European colonisation (Dean, 1997). Others have shown that colonial and post-colonial fisheries were also capable of overexploiting local organisms, causing a noticeable decline in fish and coral populations (Fogliarini et al., 2022; Sandoval Gallardo et al., 2021). Our understanding of these historical processes has predominantly relied on administrative documents, letters and accounts of European travellers and naturalists who began visiting the region in the 16th century (da Rocha, 2022; Russell-Wood, 2001; Whitehead, 2012). While certain historical sources, such as newspapers and archives, provide valuable descriptions of local plants and animals, along with their broad societal significance (Herbst et al., 2023; Sandoval Gallardo et al., 2021), many written documents produced into the late 18th century lack specific details concerning the relative abundance, distribution, and extent to which several native animals were used (Pádua, 2000). Nevertheless, these studies reinforce the growing consensus that a comprehensive understanding of current biodiversity and environmental threats necessitates information that predates the anthropogenic impacts of the most recent decades (Jackson & Hobbs, 2009; McClenachan et al., 2012).

Archaeology emerges as a discipline with the potential to illuminate the past daily experiences of vulnerable groups and minorities, as well as their interactions with the surrounding environments (Funari, 1994; Symanski, 2009; Symanski & Zarankin, 2014). Currently, Historical Archaeology in Brazil remains heavily biassed towards the analysis of ceramic artefacts, shipwrecks, infrastructure, and housing and settlement patterns (Lima, 1993; Symanski, 2009; Symanski & Zarankin, 2014), while faunal remains have received only superficial attention (Nobre, 2004). Analysis of terrestrial mammal remains can provide insights into species composition, distribution and relative abundance, as well as their function (food sources) and perceived value (economic, symbolic, etc.) to past human societies, and species responses to anthropogenic activities (Barnosky et al., 2017; Lyman & Cannon, 2017; Stahl, 2008). This last point is particularly relevant in conservation debates due to well known effects of subsistence hunting on tropical forest composition, most notably through the removal of medium- and large-bodied terrestrial mammals with low population densities (Bogoni et al., 2020; Dirzo et al., 2014; Galetti et al., 2017; Peres, 2000). Yet, little is known about these processes in historical times, nor the extent to which they may have contributed to the increasing rates of defaunation in the Atlantic Forest in recent decades (Galetti et al., 2017).

To address this knowledge gap, we present the results of zooarchaeological analyses conducted on faunal remains from colonial (prior to 1822) and post-colonial archaeological sites located in Babitonga Bay, Santa Catarina state (southern Brazil) (Figure 1). The region preserves numerous historical archaeological sites spanning from the 18th to the 20th centuries (Bandeira & Alves, 2012), whose economies depended on manioc, rice and livestock production, along with hunting and fishing in forest and mangrove ecosystems (Saint-Hilaire, 1936). Of these sites, only 15 have been excavated to date, five of which presented faunal remains. Marine and terrestrial vertebrate remains from the archaeological sites of Morro Grande 1 (MG1) and Praia Grande Unidade 21 (PG-U21) were analysed herein using an integrated approach of conventional zooarchaeological (morphological traits) analysis and collagen peptide mass fingerprinting, known as Zooarchaeology by Mass Spectrometry (ZooMS). Both sites were extensively excavated and have the largest collection of faunal remains of all the historical sites. Changes in hunting strategies through time and their putative ecological impacts were studied by comparing the historical fauna with faunal data from Pre-colonial sites in the region (Enseada I, Bupeva II, Forte Marechal Luz,

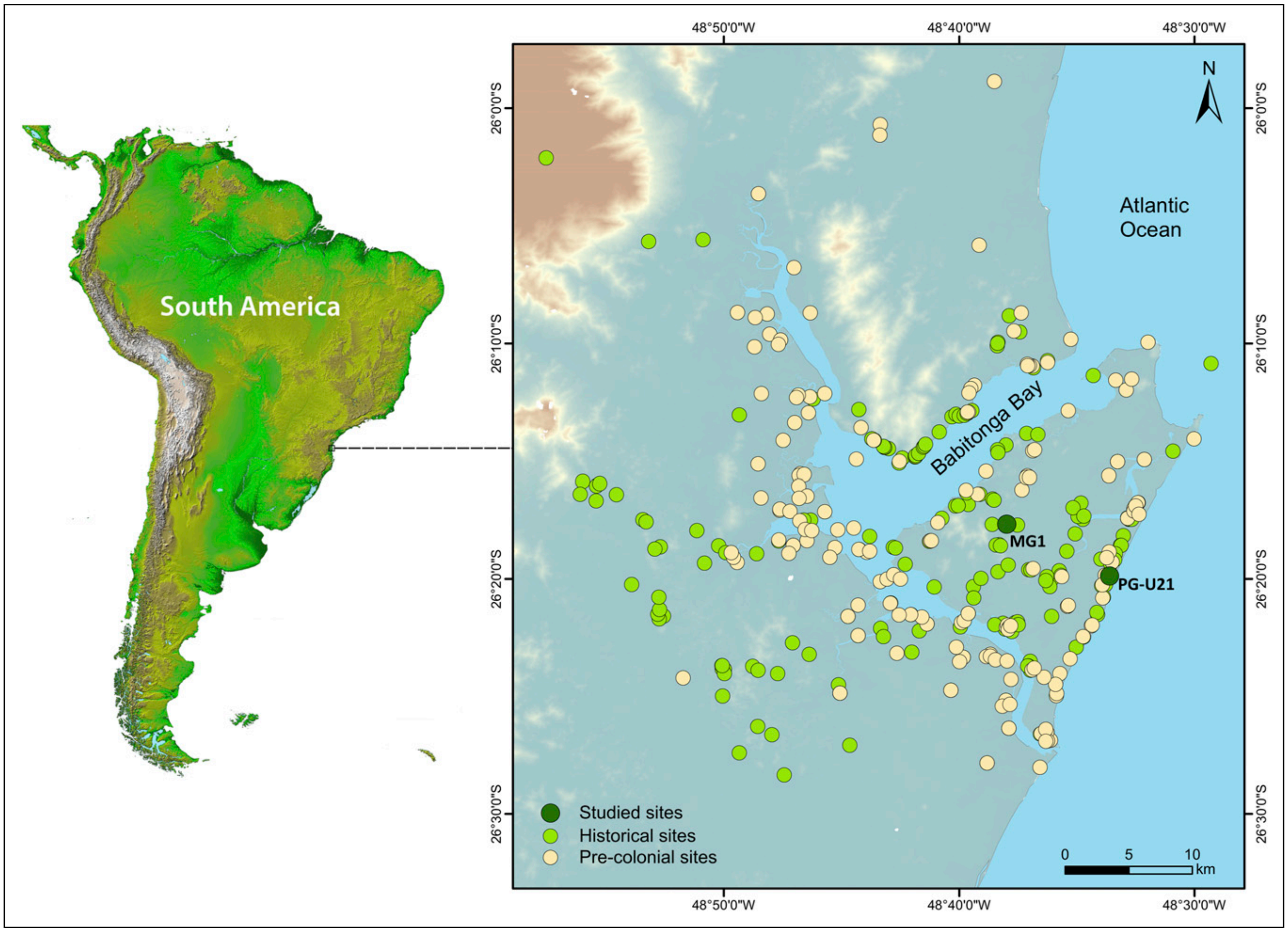

**Figure 1.** Location of Babitonga Bay in southern Brazil, including Pre-colonial and Historical sites in the region, and the two historical sites analysed herein, Praia Grande Unidade 21 (PG-U21) and Morro Grande I (MG1). Map generated on data publicly available from NASA/JPL-Caltech (adapted from https://www.jpl.nasa.gov/images/pia03388-south-america-shaded-relief-and-colored-height), Brazilian Agricultural Research Corporation - EMBRAPA (Embrapa, 2021), Natural Earth (https://www.naturalearthdata.com/), Brazilian Institute of Geography and Statistics - IBGE (https://www.ibge.gov.br/geociencias/todos-os-produtos-geociencias.html) and National Institute for Space Research - INPE (Assis et al., 2019).

Itacoara, Ilha dos Espinheiros II and Cubatão I) and from contemporary traditional coastal communities in southern Brazil, known as Caiçaras. The overarching aim of this study was to improve our understanding of the ecological footprint of colonial and post-colonial societies, and provide a historical perspective to the ongoing debates on vertebrate defaunation in the Atlantic Forest. More specifically, we aimed to understand the socioeconomic importance of marine fish and native terrestrial mammals during the historical occupation in Babitonga Bay.

## Methods

### Archaeological Contexts

MG1 and PG-U21 are situated within the municipality of São Francisco do Sul (Figure 1). Located ~10 km from the coast, MG1 holds historical significance as it is located in one of the earliest non-Indigenous colonial settlements in Babitonga Bay (Pereira, 2004). Written and oral historical records indicate that the region was primarily dedicated to cultivating manioc for flour production (Santos, 2004; Silva et al., 2001). Excavations in 2001 covering an area of 374 $m^2$ found one homogeneous stratigraphic deposit with evidence of residential spaces, ceramic artefacts and coins dated to the 19th century, and faunal remains. On the other hand, PG-U21 is considered a coastal site located in Praia Grande which exhibits a clear association with fishing. Historical accounts describe fishing and fish processing (drying) in the area, along with manioc cultivation in more recent times (Alves & Oliveira, 2002). Archaeological excavations conducted in 2002 over an area of 166 $m^2$ uncovered abundant faunal remains, ceramic artefacts dating to the 20th century, and other artefacts likely associated with residential activities (Figure 2). The stratigraphic sequence at the site encompassed six distinct layers (layers 1 to 6, with 1 being the most

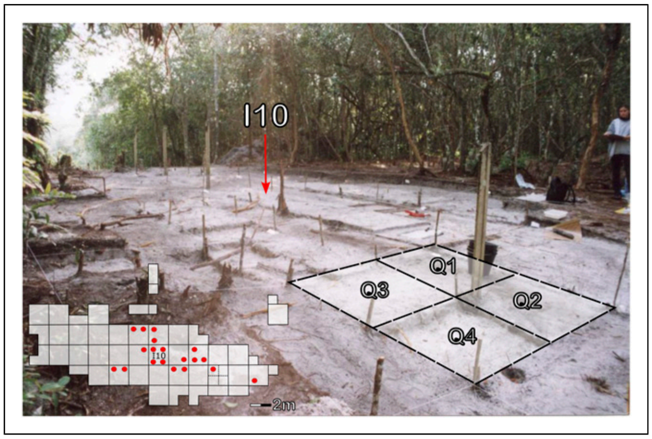

**Figure 2.** Overview of Praia Grande Unidade 21 (PG-U21) showing the excavation area (bottom left) and specific grid (I10) analysed in this study. Red points in the excavation area (bottom left) indicate the distribution of faunal remains at the site (Alves & Oliveira, 2002). The quadrants Q1, Q2, Q3 and Q4 have been depicted in grid H13 for reference to the excavation grid system used.

recent and 6 being the earliest). These layers form over time, one superimposed on the other as a result of human activities, natural processes, or a combination of both, allowing for the establishment of a chronological sequence of events and providing insight into the activities of the people who used the site.

## Sampling Strategy and Site Chronologies

Analysed faunal remains from MG1 were recovered from 77 grids, corresponding to 15.4 m$^3$ of sediment, which was sieved using a 3 mm mesh size (Silva et al., 2001). Analysed faunal remains from PG-U21 instead derived from one grid (I10) located in the centre of the excavation, accounting for 1.66 m$^3$ of sediment, which was sieved using a 2.5 mm mesh size (Alves & Oliveira, 2002). Although only vertebrate remains were analysed from both sites, a significant number of marine mollusc shells (e.g. *Anomalocardia flexuosa*) were also recovered at PG-U21 (Alves, 2003; Alves & Oliveira, 2002) and are currently undergoing analysis.

In order to improve the chronological attributions of MG1 and PG-U21, bones of terrestrial mammals (n = 4) were selected for radiocarbon dating (AMS) at CEDAD, Università di Salento (Italy). Bones from MG1 (one deer and one cattle bone) were sampled from layer 1 (grids A12 [LTL22552] and C13 [LTL22553]). Bones from PG-U21 (one armadillo and one cattle bone) were sampled from layer 2 (LTL22550) and layer 3 (LTL22551) in grid I10. Conventional radiocarbon dates were calibrated using OxCal v. 4.4 (Ramsey, 2009), using the 100% atmospheric calibration curve for the southern hemisphere, SHCal20 (Hogg et al., 2020). Calibrated dates were rounded to 10 years.

## Archaeological Faunal Identification

The vertebrate faunal remains were identified through side-by-side comparison with reference collections from the Museu Arqueológico de Sambaqui de Joinville (MASJ, Brazil), the Laboratório de Arqueologia e Patrimônio Arqueológico at the Universidade da Região de Joinville (LAPArq/Univille, Brazil) and the Laboratory of Archaeozoology at the Universitat Autònoma de Barcelona (Spain); along with specialised literature (Adams & Crabtree, 2012; France, 2009; McLelland, 1991; Sebben et al., 2019; Tercerie et al., 2022; Wensing, 2009). The scientific names followed the World Register of Marine Species (Horton et al., 2020) and the Animal Diversity Web (Myers et al., 2020). The abundance of species was represented by the Number of Identified Specimens (NISP), a quantitative unit frequently used in zooarchaeological studies (Grayson, 1984; Lyman, 2008a, 2018). The Number of Specimens (NSP), which represents the total of all analysed specimens (identified or unidentified), and the Number of Unidentified Specimens (NUSP) were also quantified. Fragments of the same specimen that could be refitted were counted as one. Species richness (SR) was calculated using the Minimum Level of Taxonomic Identification, considering only the minimum hierarchical level for a particular taxa. In order to account for variations in the excavation areas and in the volume of archaeological deposits between the sites, as well differences in the number of bones and taphonomic processes that may variably affect distinct taxonomic groups (Lyman, 2008b; Reitz & Wing, 2008), the NISP was standardised for the volume of sediment (NISP/m$^3$). This index provides an independent density measurement for each taxonomic class.

Fish remains were separated between postcranial (posterior to the first precaudal vertebrae) and cranial (neurocranium and viscerocranium) bones for skeletal frequency analysis, which provides insight into processing techniques (e.g. parts removed during fish processing for storage, trade, etc.) (Lyman, 1994; Zohar et al., 2001). Other taphonomical features such as fragmentation, heat exposure, and cut marks were also recorded (Costamagno et al., 2019; Egeland, 2003; Fernandez-Jalvo & Andrews, 2016; Yravedra, 2013). Remains that were slightly broken (e.g. vertebra without spinous and transverse processes) were considered whole.

## Faunal Identification Using Collagen Peptide Mass Fingerprinting (ZooMS)

According to historical records both cattle (*Bos taurus*) and buffalo (*Bubalus* spp.), as well as peccary (Tayassuidae) and domestic pig (Suidae), were exploited in the region. Chickens (*Gallus gallus*) were also commonly exploited along with other native birds. The remains of these morphologically similar species are complex to set apart using conventional morphological analysis, requiring additional analytical approaches to achieve accurate identifications. As such, the remains of 57 mammals and birds from MG1 (n = 30) and PG-U21 (n = 27) were selected for analysis with Zooarchaeology by Mass Spectrometry (ZooMS) to confirm the morphological taxonomic identification. ZooMS is a method of peptide mass fingerprinting that takes advantage of interspecies differences in the amino acid sequences of collagen to make taxonomic identifications (Buckley et al., 2009; Welker et al., 2015).

Bone samples, ranging from 10-30 mg, were sampled from each of the 57 remains and put in 250 µl of 0.6 M hydrochloric acid (HCl) at 4°C to demineralize. The acid was then removed and the samples were rinsed once in 0.1 M sodium hydroxide (NaOH) to remove humic contaminants, followed by three washes with 200 µl of 50 mM ammonium bicarbonate buffer (AmBic, $NH_4HCO_3$, pH 8). After the final rinse, 200 µl of AmBic was added and the samples were gelatinized for 1 hour at 65°C. 125 µl of each sample was transferred to a 96 well plate and the samples were digested overnight at 37°C with the addition of 0.4 µg of trypsin. Samples were acidified to 0.1% trifluoroacetic acid (TFA) to stop the trypsin, then purified using C18 resin ZipTip pipette tips (Pierce™ Thermo Scientific) via an Opentrons OT-2 pipetting robot using an in-house Python script. The in-house Python script used the Opentrons Gen 1 300 µL multichannel pipette, three 96 well plates and a 12 reservoir plate in order to purify peptides using the C18 Zip Tips. The dimensions of the C18 Zip Tips and accompanying tiprack were added to the robot as a custom labware definition to allow the robot to recognise and use the C18 Zip Tips. 1 µl of the extracted peptides was spotted onto a Bruker target plate and combined with 1 µl of matrix solution (α-cyano-hydroxycinnamic acid) then analysed in triplicate along with calibration standards on a Bruker ultrafleXtreme MALDI TOF/TOF mass spectrometer at the University of York. Spectra were averaged and analysed using mMass software (Strohalm et al., 2008) and species were determined based on published *m/z* markers (Buckley et al., 2009, 2014, 2017; Eda et al., 2020, 2023; Kirby et al., 2013; Welker et al., 2015) and in some cases using known reference material (unpublished data, see SM4 Table 3).

## Comparing Native Terrestrial Mammal Functional Traits Across Time Periods

Differences in mean body weight classes (body mass), population density, and trophic groups of targeted non-volant terrestrial mammal species were compared across three time periods: Pre-colonial (4500–1150 cal BP), Historical (1750-1950 AD) and Contemporary (1998-2000 AD). These differences were also compared with the current composition of native terrestrial mammals in the region, against which we assessed the degree of selection in past hunting activities. Pre-colonial assemblages (4500–1150 cal BP) were compiled from archaeological sites located in Babitonga Bay: Enseada I, Bupeva II, Forte Marechal Luz, Itacoara, Ilha dos Espinheiros II, and Cubatão I (Bandeira, 1992, 2004; Benz, 2000; Bryan, 1993; Fossile et al., 2019). Historical assemblages (1750-1950 AD) included species recovered from MG1 and PG-U21, both located in Babitonga Bay. We also compared the Pre-colonial and Historical faunal assemblages with hunted animals among three *Caiçara* communities on the southeastern coast of Brazil (~150 km from Babitonga Bay) between 1998 and 2000 (Hanazaki et al., 2009). This Contemporary assemblage (1998-2000 AD) derived from interviews with Caiçara groups who descend from Indigenous, African and European populations, and thus may serve as a modern analogue for assessing patterns of animal exploitation in historical times (Begossi, 2006; Begossi & Richerson, 1993; Hanazaki & Begossi, 2003). Present day Caiçara communities value native terrestrial mammals such as deer (*Mazama* spp.), lowland paca (*Cuniculus paca*), agouti (*Dasyprocta azarae*), armadillo (*Dasypus novemcinctus*), opossum (*Didelphis aurita*), capybara *(Hydrochoerus hydrochaeris*), tamandua (*Tamandua tetradactyla*), and peccary (*Pecari/Dicotyles tajacu*) as dietary sources (Begossi & Richerson, 1993; Hanazaki et al., 2009). Certain species, including deer, capybara, peccary and also ocelot (*Leopardus pardalis*), are also exploited for medicinal purposes (Hanazaki et al., 2009). Data on native non-volant terrestrial mammals was obtained from surveys performed in Babitonga Bay between 1909 and 2016 (Carvalho-Junior, 2022; Cherem et al., 2004; Dornelles et al., 2017; Ima, 2009) and complemented by the aforementioned archaeological data, resulting in a total of 53 species.

Mean body weights were determined for each species based on data from the literature (e.g. Myers et al., 2020), and categorised into small (<1 kg), medium (1-15 kg), and large mammals (>15 kg) following Galetti et al. (2017) and Vynne et al. (2022). Population density (individuals/km$^2$) and trophic groups were compiled from Robinson & Refford (1986) and, when required, complemented with information from other literature (Duarte et al., 2012; Faria-Corrêa, 2004; Galante & Cassini, 1994; Myers et al., 2020; Reis et al., 2006; Tomas & Desbiez, 2004). Density data was obtained for a total of 46 species. The average density was calculated following Galetti et al. (2017), using game species found in each analysed period.

Species were divided into trophic categories of Carnivore, Myrmecophagy, Insectivore-omnivore, Frugivore-omnivore, Frugivore-granivore, Frugivore-herbivore, Herbivore-browser, Folivore-herbivore, and Herbivore-grazer (Reis et al., 2006; Robinson & Redford, 1986). The statistical significance in the proportions of analysed traits across time periods was tested using a two-tailed Binomial test ($p < 0.05$) in RStudio Software (RStudio Team, 2020).

# Results

## Site Chronologies

Terrestrial mammal samples from MG1 and PG-U21 provided calendar ages ranging from 1510-1800 to 1690-1950 AD (68.4% confidence interval), with medians ranging from 1650 to 1850 AD (Table 1, Figure 3A). Overall, the calibrated

**Table 1.** Radiocarbon chronology and contextual information of archaeological bone samples.

| Site | CEDAD Lab code | Material | Context | $^{14}$C yr. BP | $^{14}$C yr. cal AD (2σ) | Median cal AD |
|---|---|---|---|---|---|---|
| PG-U21 | LTL22550 | Bovidae | Grid 110-Q1, Layer 2 | 281 ± 45 | 1510 – 1800 | 1660 |
| PG-U21 | LTL22551 | Dasypodidae | Grid 110-Q3, Layer 3 | 139 ± 40 | 1690 - 1950 | 1850 |
| MG1 | LTL22552 | Cervidae | Grid A12, Layer 1 | 282 ± 40 | 1510 - 1800 | 1650 |
| MG1 | LTL22553 | Bovidae | Grid C13, Layer 1 | 175 ± 40 | 1670 - beyond calibration range | 1810 |

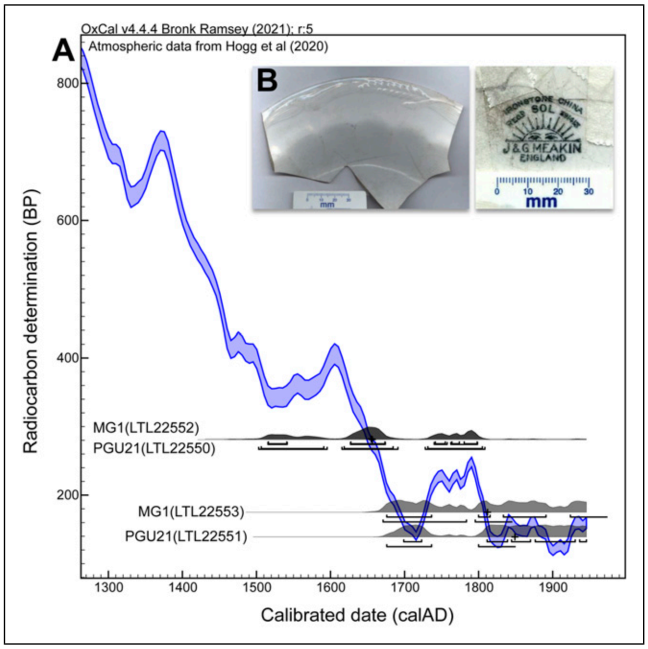

**Figure 3.** A) Radiocarbon chronology and B) associated material culture (fragment of J&G Meakin Ltd. pottery from PG-U21 with the distinctive impression dated to the 1910's).

radiocarbon dates were older than the associated material culture from both sites (coins, tin cans and ceramic artefacts), which have been assigned to the 19th and 20th centuries (Alves & Oliveira, 2002; Silva et al., 2001). For example, fragments of English pottery produced by J&G Meakin Ltd. with a distinguishing "SOL" stamp, were found in layers 1 and 2 of PG-U21 (Figure 3B). This particular make of pottery appears to have been produced from the 1910's, thus offering a *terminus post quem* for the uppermost part of the site. Similarly, diagnostic pottery remains and coins found at MG1 indicate that some occupations took place from 1821 AD. Although it is possible that the radiocarbon dates detected earlier occupations (i.e. 1700 AD), their large probabilistic distributions combined with the plateau-reversals in the $^{14}$C calibration curve around 1700-1800 AD and 1820-1920 AD (Manning et al., 2018; Taylor et al., 1996), complicate the radiocarbon interpretation and impinge upon our ability to precisely constrain the site chronologies (Figure 3A). The combination of radiocarbon and relative material-based chronologies, therefore, led us to assign a parsimonious age for both sites of 1750-1950 AD.

## Species Composition, Distribution and Relative Abundance

A total of 11262 bone remains (NSP) were analysed from MG1 and PG-U21, of which 10960 (97.32%) could be identified using distinct taxonomic levels (NISP) and 302 (2.68%) could not be identified (NUSP) (SM1), due to pre- and/or post-depositional alterations (SM2). 57.90% of the remains analysed from MG1 were fragmented, and 52.43% of remains were fragmented from PG-U21. Cutmarks were identified on 76.92% of native terrestrial mammal bones (excluding osteoderms and teeth), ranging from 4.92% in *Didelphis* spp. (opossum) and *Cuniculus paca* (lowland paca) to 12.30% in Dasypodidae (armadillo). Cutmarks were also found on 80% of domesticated animal bones (excluding teeth) from MG1 and PG-U21, including Bovidae (36.81%) and Ovicaprid (1.39%). While Suina (pig and/or peccary) presented cutmarks in 90.91% of the remains. In both cases, the cutmarks were mostly located on limb bones (e.g., tibiae, metapodial and phalange), which can be related to carcass skinning, defleshing and disarticulation (Costamagno et al., 2019; Egeland, 2003). Cutmarks confirm that native terrestrial mammal remains from both sites resulted from anthropogenic activities (e.g. hunting) rather than being a natural death assemblage.

Bony fish (NISP = 9002 remains) from MG1 and PG-U21 together accounted for 82.13% of the faunal remains, including *Genidens barbus* (white sea catfish), *Conodon nobilis* (barred grunt), *Centropomus* spp. (snook), *Cynoscion* spp. (weakfish), *Cynoscion leiarchus* (smooth weakfish), *Larimus breviceps* (shorthead drum), *Micropogonias furnieri* (whitemouth croaker) and *Pogonias courbina* (black drum). Fish remains were mostly represented by postcranial bones in both MG1 (n = 180, 84.11% fish remains) and PG-U21 (n = 3552, 71.35% fish remains) in relation to cranial bones (MG1, n = 34, 15.89%; PG-U21, n = 1426, 28.65%). The cranial/postcranial (C/P) ratio from aggregated archaeological layers differed between MG1 (0.19) and PG-U21 (0.40) (SM3; Figure 4).

Fish remains were followed by mammals (16.45%, NISP = 1803), with medium-bodied mammals represented by *Didelphis* spp. (opossum), Dasypodidae (armadillo), Cebidae (capuchin monkey) and *Cuniculus paca* (lowland paca), while large mammals were represented by Suina (Tayassuidae (peccary) and/or Suidae (domestic pig)), Cervidae (deer) and Bovidae (cattle). Birds (1.41%; NISP = 154) were

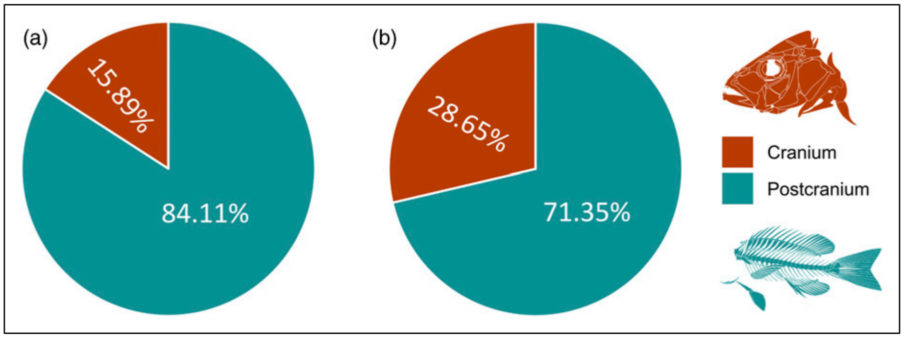

**Figure 4.** Aggregated relative frequency of cranial and postcranial fish bones from (A) MG1 and (B) PG-U21. Figure generated on data publicly available from ArchéoZoo.org (https://www.archeozoo.org/archeozootheque/).

represented by Aves (cf. *Gallus gallus* [chicken]). The sole species of cartilaginous fish (0.01%; NISP = 1) recorded was *Carcharhinus* spp. (shark) (SM1).

## MG1

When assemblages were analysed individually MG1 had a total of 1136 identified remains (74/m$^3$), of which 53.26% (NISP = 605) corresponded to indeterminate mammals (Mammalia), followed by indeterminate bony fish (Actinopterygii; 16.11%; NISP = 183), then cattle (6.78%; NISP = 77), pig (peccary and domestic pig) (6.25%; NISP = 71), deer (2.73%; NISP = 31), rodents (2.73%; NISP = 31), bird (cf. *Gallus gallus*; 2.02%; NISP = 23) and others (<2%) (SM1).

The highest species richness in MG1 was represented by mammals (SR = 10), including both native (deer, lowland paca, armadillo, opossum, dolphin and cf. whale) and domestic (cattle and sheep) species. The remains of marine mammals (Delphinidae and cf. Mysticeti) appear mostly as artefacts, due to indications that they were intentionally polished and/or modified, such as the presence of nails in two Delphinidae remains. ZooMS analysis confirmed the overall morphological identifications at MG1 (86.7% congruence), with the exception of three Suina which ZooMS identified as two cattle and one brocket deer, and one cattle that ZooMS identified as brocket deer (SM4 Table 1). Along with confirming the exploitation of cattle (*Bos taurus*, n = 11), brocket deer (*Mazama* spp., n = 12), and probably chickens (*Gallus gallus*, n = 2, although the spectra were of poor quality so a confident identification was not possible), ZooMS also allowed us to verify that both peccary (*Tayassu pecari and/or Pecari/Dicotyles tajacu*, n = 4) and domestic pig (*Sus domesticus*, n = 1) were exploited at the site (SM4 Table 1). Suines can be difficult to distinguish between as different species of *Sus*, for example, have highly similar collagen sequences meaning it is often impossible to determine if wild or domestic pigs were being exploited. Using several known peccary (*Tayassu pecari*, *Pecari*/*Dicotyles tajacu*) reference bones, differences were identified in the MALDI-TOF-MS spectra compared to *Sus* spp., with peccary having peptide markers at *m/z* 1991 and 2959, and *Sus* spp. with markers at *m/z* 1961 and 2987 (SM4 Figures 1, 2 and 3). While these markers need to be confirmed with further analyses, including LC-MS/MS sequencing to identify the specific peptides, they were identified in the six Suina samples analysed herein (SM4 Figures 2 and 3), and also in several additional peccary (*m/z* 1991, 2959) and pig (both domestic and wild boar, *m/z* 1961, 2987) samples from other sites unrelated to this study. Additionally, bulk collagen isotope analysis performed on these Suina samples as part of an ongoing study (data not presented herein) provides further support that these additional peaks can be used to distinguish between *Sus* and Tayassuidae, as the two identified as domestic pig (one from MG1 and one from PG-U21) had nitrogen stable isotope ($\delta^{15}$N) values of 11.03‰ and 8.09‰, respectively, while the samples identified as peccary (all from MG1) had significantly lower values, ranging from 1.32‰ to 1.70‰, suggestive of different trophic ecologies.

## PG-U21

A total of 9825 remains (5918/m$^3$) were recovered from PG-U21, of which 74.19% were indeterminate bony fish (Actinopterygii, NISP = 7288), followed by armadillo (8.48%, NISP = 833 including osteoderms), barred grunt (7.99%, NISP = 785 including otoliths), whitemouth croaker (3.31%, NISP = 325 including otoliths), and others (<2%) (SM1). Several species including cattle (n = 10), chicken (n = 9), armadillo (n = 9), and domestic pig (n = 1) were all identified with ZooMS (SM4 Tables 1 and 2). This represents 96.3% consistency with morphological identifications, with the exception of one sample morphologically identified as armadillo but that could not be identified amongst the species with currently available ZooMS collagen peptide markers.

The composition, relative abundance and density of faunal remains of PG-U21 varied considerably through the stratigraphy. Fish remains were recovered from all layers, but a noticeable increase in the density of remains (NISP/m$^3$) was documented in layers 1 and 2, possibly reflecting fishing intensification (Figure 5). These were mostly represented by

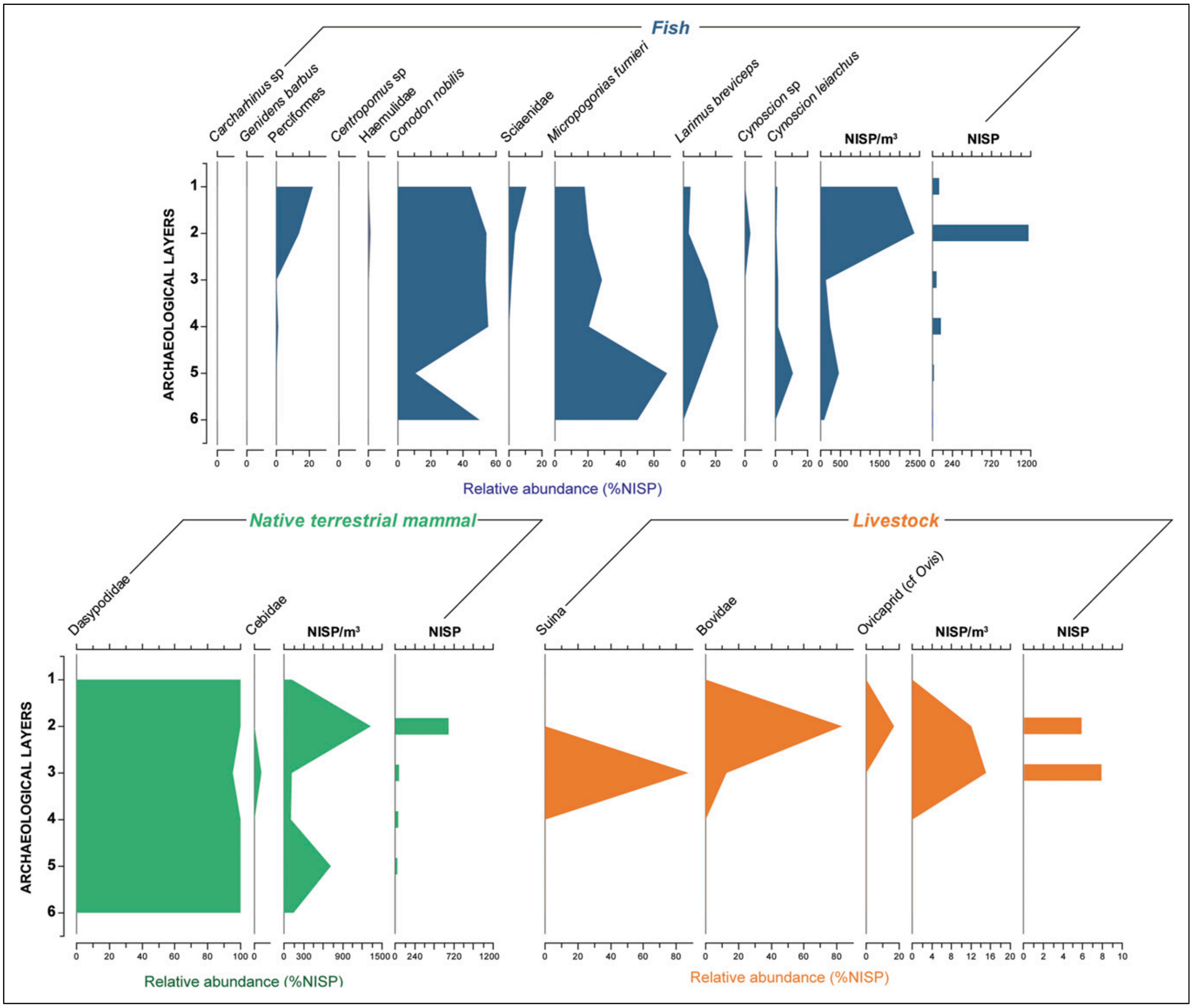

**Figure 5.** Stratigraphic variation in the relative abundance (%NISP), density (NISP/m³) and number of identified remains (NISP) for fish, native terrestrial mammals, and livestock from PG-U21, excluding the generic attributions to Actinopterygii and Mammalia, and remains of Aves. Based on the ZooMS identifications, Suina were grouped with livestock.

barred grunt and whitemouth croaker, followed by shorthead drum and others. Remains of native terrestrial mammals were also found in all layers, represented mostly by armadillo and a few remains of capuchin monkeys. Interestingly, their densities also increased in layer 2. By contrast, livestock (cattle, sheep, domestic pig) were only documented in layers 3 and 2, with the highest density in layer 3. Finally, bird (mostly believed to be chicken) remains were found in all layers, with higher densities in layers 3, 4 and 5.

## Trait Variation in Native Terrestrial Mammals Across Time Periods

A total of 21 native terrestrial mammal species were identified across the three studied time periods, with body weight classes ranging from 0.6 kg to 200 kg (SM5; Figure 6A). Among these, 20 species were documented for the Pre-colonial period (4500–1150 cal BP, SM6), six for the Historical period (1750-1950 cal AD), and 10 for the Contemporary period (1998-2000 AD). In the Pre-colonial period, the species with the largest and smallest mean body weights were *Tapirus terrestris* (Brazilian tapir, 200 kg) and *Cavia aperea* (Brazilian guinea pig, 0.6 kg), respectively. In the Historical period, MG1 exhibited a broader range of body weight classes (1.3 kg to 30.5 kg), while PG-U21 had a more restricted range (2.8 kg to 5.7 kg). Tayassuidae (peccary, 30.5 kg) had the largest mean body weight, while Didelphis spp. (opossum, 1.3 kg) was found to have the lowest. In the Contemporary period, the largest mean body weight was represented by *Hydrochoerus hydrochaeris* (capybara,

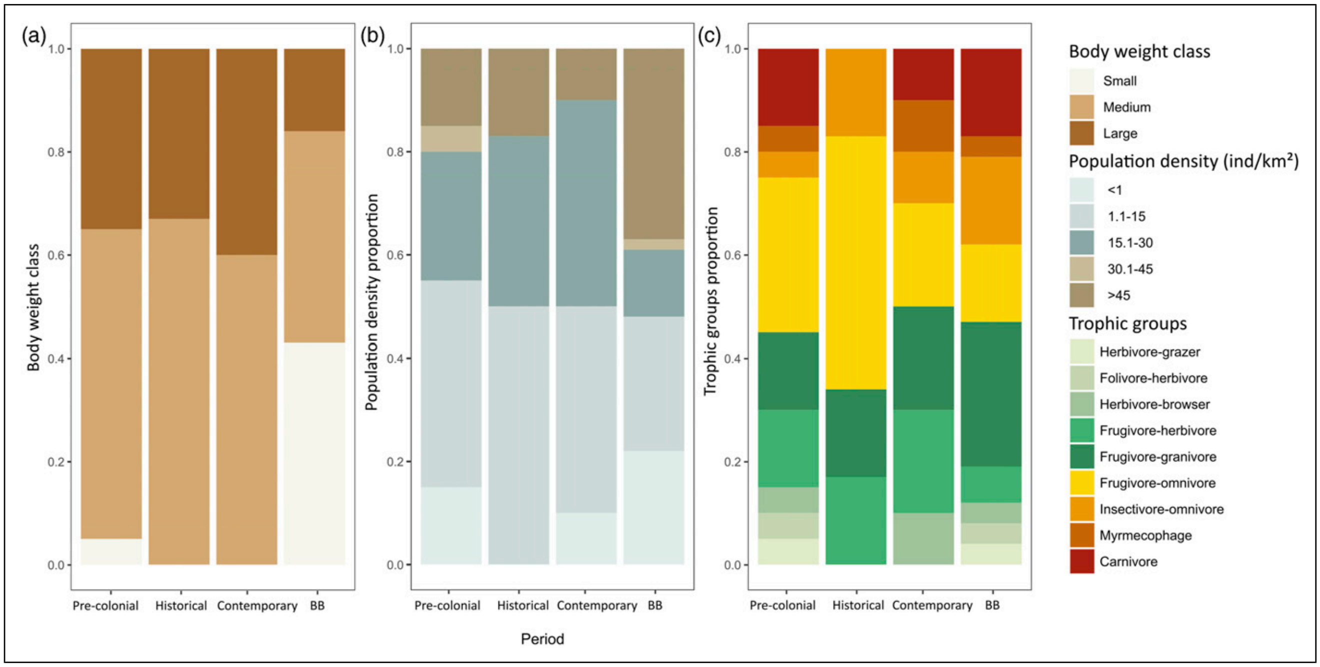

**Figure 6.** Mammalian traits and functional groups across studied time periods. The proportion of mammal species differentiated by (A) body weight classes, (B) population density (individual/km$^2$) and (C) trophic group between Pre-colonial (4500–1150 cal BP), Historical (1750-1950 cal AD) and Contemporary (1998-2000 AD) periods, along with the current native terrestrial mammal composition of Babitonga Bay (BB).

50.5 kg), while the species with the lowest mean body weight was *Didelphis aurita* (big-eared opossum, 1.3 kg). The current composition of terrestrial mammals from Babitonga Bay includes species with a broader range of body weight classes, ranging from the Brazilian tapir (200 kg) to *Monodelphis iheringi* (Ihering's short-tailed opossum, 0.1 kg).

Medium-bodied mammals (1.01-15 kg), accounting for 41% of the current species in Babitonga Bay, were the most exploited animals during all studied periods, ranging from 60% in the Pre-colonial and Contemporary periods, to 67% in the Historical period. These were followed by large-bodied mammals (> 15.1 kg) ranging from 30% in the Contemporary, 33% in the Historical, to 35% in the Pre-colonial period; while evidence for targeting small-bodied mammals (< 1.0 kg) was only detected in the Pre-colonial period, represented by Brazilian guinea pig. When considering the current species composition of Babitonga Bay in comparison to the three time periods and body weight classes studied, significant differences were only observed for the proportion of small-bodied mammals between the Pre-colonial period and the current composition ($p = 0.01367$).

Targeted mammals had population densities ranging from 0.1 to 65.5 individuals/km$^2$, with the highest density represented by the Brazilian guinea pig (65.5 individuals/km$^2$) and the lowest by *Puma concolor* (cougar) (0.1 individuals/km$^2$). In contrast, all native terrestrial mammals had estimated density values ranging from 0.1 to 400 individuals/km$^2$. However, the majority of targeted mammals across all periods exhibited densities ranging from 1.1 to 30 individuals/km$^2$. These species represented 68% of the terrestrial mammals in the Pre-Colonial period, 83% in the Historical period, and 80% in the Contemporary period. By contrast, these species represent only 39% of Babitonga Bay's current terrestrial mammal composition, which shows density distributions ranging from 0.1 to 400 individuals/km$^2$ (SM5; Figure 6B). Although no significant differences were observed across the studied periods, the results suggest that Pre-colonial, Historical and Contemporary hunting practices selectively targeted medium- and large-bodied animals with low to medium population densities.

Regarding trophic groups, the categories ranged from Herbivore-grazers to Carnivores, with the majority of targeted mammals belonging to the Frugivore-omnivore category (SM5; Figure 6C). The highest diversity of trophic categories was detected in the Pre-colonial period, with a preference for Frugivore-omnivores (30%), followed by Carnivores (15%), Frugivore-granivores (15%), Frugivore-herbivores (15%), and others at less than 5%. In the Historical period, the exploitation was mainly focused on Frugivore-omnivores (n = 49%), followed then by Insectivore-omnivores, Frugivore-granivores and Frugivore-herbivores (all with n = 17%). In the Contemporary period, the most exploited category was again Frugivore-omnivores, Frugivore-granivores and Frugivore-herbivores (all with n = 20%), followed by Carnivores, Myrmecophages, Insectivore-omnivores and Herbivore-browsers (all with n = 10%). The current terrestrial mammal composition of Babitonga Bay exhibits the same trophic groups as those in the Pre-colonial and Historical periods; however, the most abundant trophic group is Frugivore-granivores (28%), followed by Carnivores (17%), Insectivore-omnivores (17%), Frugivore-omnivores (15%), Frugivore-herbivores (7%), Myrmecophages (4%), and others. Despite the preference for Frugivore-omnivore species in the Pre-colonial, Historical and Contemporary periods, there were no statistical differences between periods and current compositions.

## Discussion

Radiocarbon dates and artefacts indicate that MG1 and PG-U21 were occupied from approximately 1750 to 1950 AD, one hundred years after the establishment of the village of *Nossa Senhora da Graça* on the São Francisco River in 1658 (Cabral, 1937; Saint-Hilaire, 1936). In 1660, the village was elevated to the status of town, and in 1665 it was designated as a parish, and then as a city in 1847, the earliest city in the state of Santa Catarina (Cabral, 1937). Faunal remains from MG1 and PG-U21 offer valuable insights into the livelihoods and the ecological footprints of these early colonial and post-colonial decades in Babitonga Bay. The information gained also allows us to reassess the often neglected role of fisheries during the early modernization of Brazil's southern coast.

The zooarchaeological data revealed noticeable differences in faunal remains between MG1 and PG-U21, both in terms of species composition, relative abundance and density (Figure 7A-B). We acknowledge that differences in recovery and analytical methods can affect fundamental and derived measurements of archaeological faunal remains (Grayson, 2014; Lyman, 2008a; Reitz & Wing, 1999); however, these are unlikely to explain the variations seen among the sites. Firstly, in both sites, faunal remains were retrieved using similar mesh sizes (2.5 and 3 mm), which are considered adequate for the recovery of small fragments and anatomical parts, such as fish remains (McKechnie & Moss, 2016; Zohar & Belmaker, 2005). Secondly, taxonomic identification for both sites was performed using the same reference collections and by the same analyst, therefore reducing analytical biases. Moreover, the proportion of fragmented bones was similar among sites. The recovered faunal remains thus confidentially reflect fundamental differences in subsistence and economic activities between the sites.

Fish outnumbered other faunal remains at PG-U21, with an overall aggregate density (899/m³) comparable to, or higher than, some local Pre-colonial shell mounds (known as *sambaquis*, with densities from $42/m^3$ to $7871/m^3$) produced by groups subsisting largely on fishing (Fossile et al., 2019, 2023) (Figure 7B). Fishing intensification, however, appears to have occurred during the later phases of the site dated to the early 20th century. This coincides with a time interval of substantial policy incentives for commercial fisheries, with increased catches and fishing efforts along the coast of Santa Catarina state (Herbst et al., 2023; Sandoval Gallardo et al., 2021); as such, this fishing intensification at PG-U21 may reflect a local response to increased market demand. The relatively low taxonomic diversity of fish remains suggests specialised fishing practices aimed at supplying both household and local markets, which is largely supported by historical accounts documenting the importance of fish as a source of food and income in Babitonga Bay since the mid-19th century (Saint-Hilaire, 1936). The most frequently caught species (whitemouth croaker and barred grunt) continue to display high economic and subsistence values today (Haimovici et al., 2016; Lima et al., 2019), and the same fish species are also consumed by contemporary Caiçara communities along the Atlantic Forest coast (Begossi, 2006; Begossi & Richerson, 1993; Hanazaki & Begossi, 2003). Extensive research has demonstrated that these communities carefully consider the costs and benefits associated with pursuing and processing food resources based on factors such as site location, environmental conditions, and the influence of urban centres and markets (Hanazaki & Begossi, 2000; MacCord & Begossi, 2006). According to this theoretical proposition, there is a stronger focus on fishing as the proximity to the coast increases, which explains the higher dependence on fishing observed in PG-U21 (coastal) compared to MG1 (inland). Overall the results highlight the significant role of fishing in Babitonga Bay between the 18th and the 20th century, which adds to the growing evidence for a heavy reliance on fishing for food security for thousands of years in the region (Fossile et al., 2019, 2023; Toso et al., 2021). This is particularly significant given that fishers were often overlooked or inadequately represented in regional historical narratives (Silva, 1988, 2001).

The species found at PG-U21 and MG1 suggest that fishing was mainly practised in coastal waters. Surprisingly, other coastal species widely captured nowadays, such as mullets (Hanazaki & Begossi, 2000, 2003; Herbst & Hanazaki, 2014; Sandoval Gallardo et al., 2021), have not been recorded at either site. *Mugil liza* (Lebranche mullet), in particular, is abundantly caught along the southeastern coast of Brazil during austral autumn and winter, from May to July (Steenbock, 2019), and this practice has been regionally documented since the early 16th century (Staden, 2020). It is possible that the species was not consumed by local residents, as observed among some contemporary communities in southern Brazil (Hanazaki & Begossi, 2003). Alternatively, processing methods involving salting and drying (locally known as *cambira*, (Alves, 2003; Anacleto et al., 2019)) may have prevented the survival of diagnostic bone remains in the archaeological record. *Cambira* involves a longitudinal incision along the dorsal region of the individual, and the removal of the head, prior to salting and drying. This method is similar to the one observed by Zohar and Cooke (Zohar & Cooke, 1997) in the northwest of Panama Bay, who demonstrated that it causes damage to, and loss of, cranial bones, precisely those bones which contain most of the diagnostic

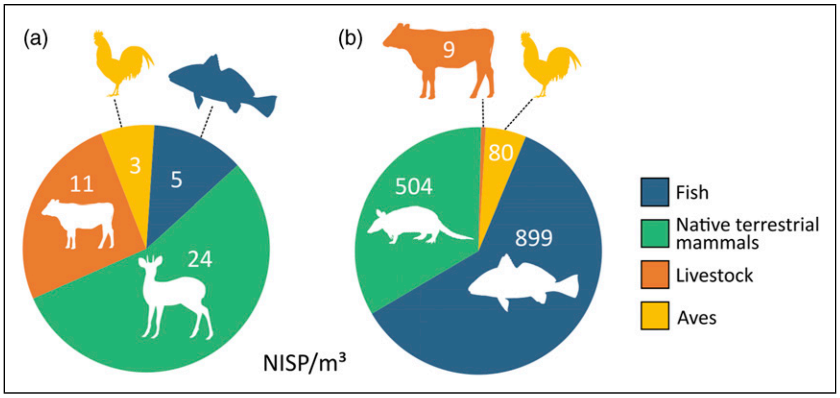

**Figure 7.** Aggregated density (NISP/m³) for fish, native terrestrial mammals, livestock and birds from (A) MG1 and (B) PG-U21, excluding the generic attributions to Actinopterygii and Mammalia. For MG1, remains of Artiodactyla and Canidae were also excluded from the analysis. Based on the ZooMS identifications, Suina were grouped with native terrestrial mammals for MG1 and with livestock for PG-U21. Figure generated on data publicly available from PhyloPic (http://phylopic.org/).

elements needed for taxonomic identification. Nevertheless, the differences in cranial/postcranial values between the two sites and the absence of otoliths in MG1 suggest that a large number of fish may have been locally processed in PG-U21, while in MG1 more fish were brought to the site already processed (with crania removed). As such, processing methods are unlikely to explain the absence of mullets at least in PG-U21, unless the species was processed and cranial bones disposed of elsewhere, with only the postcranial fraction transported to the site for consumption or trade. The absence of mullets, therefore, remains a matter deserving of further study.

Our results indicate that livestock did not play a major role as a food source (e.g. meat), nor as sources of secondary products (dairy, fur/hide) during the colonial and post-colonial periods in Babitonga Bay (Figure 7A-B). Rather, local food security and livelihood relied on fishing and the hunting of native terrestrial mammals, along with crop agriculture. Fish were exploited for their meat, fat and oil, while native terrestrial mammals could have also been pursued for their secondary products (fur/hide), as suggested by the number and location of cutmarks. This is supported by historical records which report that fish and native terrestrial mammals were consumed at the household level, and used as sources of income (Ribeiro & Corção, 2013; Saint-Hilaire, 1936). Among domesticated animals, chickens are an exception as they very likely played a role as a daily source of dietary protein (meat and eggs) at both sites, as documented among traditional riverine and coastal communities nowadays (Hanazaki & Begossi, 2003). Fish, native mammals and chickens appear to have contributed substantially to the overall economy of PG-U21. By contrast, the low density of faunal remains in MG1 suggests that other economic activities, such as plant cultivation and processing (e.g. manioc milling), prevailed at the site.

## Long-Term Selective Hunting in Babitonga Bay

Native terrestrial mammals made up a significant proportion of faunal remains at both sites. This suggests that species currently undergoing population declines were exploited in the region for at least the past two centuries. When comparing this data to information gathered from Pre-colonial sites, our findings show a consistent pattern of medium- and large-bodied terrestrial animal species being hunted by both Pre-colonial and historical coastal communities in Babitonga Bay (Brazilian tapir, and various species of deer and peccary). This hunting trend persists despite changes in the purpose of hunting over different study periods, such as subsistence, ritualistic, and livelihood pursuits. Such a pattern is also observed among some contemporary Caiçara communities, and has been extensively documented in tropical forests in South America and beyond (Ceballos et al., 2017; Darimont et al., 2023; de Souza & Alves, 2014; Dirzo et al., 2014; Milner-Gulland & Bennett, 2003; Peres, 2000).

Significantly, several species identified in the Pre-colonial and Historical periods, such as Pampas deer (*Ozotoceros bezoarticus*) (Bryan, 1993), Brazilian tapir, white-lipped peccary, and red brocket deer are no longer documented in the region (Carvalho-Junior, 2022; Dornelles et al., 2017). The last recorded sightings of tapirs and peccaries in Babitonga Bay date back to 1996, while the last record of a red brocket deer was in 2001 (Cherem et al., 2004). By contrast, these species have been reported between 2015 and 2019 in a Protected Area located approximately 45 km away from Babitonga Bay (Hübel et al., 2021), reinforcing the role of conservation strategies in reducing defaunation (Bogoni et al., 2020). Despite a long history of hunting, Babitonga Bay shows a notable diversity of medium and large terrestrial mammal species (n = 30, excluding volant mammals), surpassing the average observed in the Atlantic Forest from 1983 to 2017 (n = 14.7 species) (Bogoni et al., 2018). This suggests that the remaining forested areas may still be capable of sustaining levels of productivity that offset the detrimental effects of hunting and habitat degradation (Peres, 2000; Peres & Nascimento, 2006).

When considering the average density of mammals, our results suggest hunting intensity was lower in the Historical period (22.1 ind./km$^2$), compared to both the Contemporary (18.5 ind./km$^2$) and Pre-colonial periods (18 ind./km$^2$). These subtle differences could be attributed to the relatively smaller human population residing in Babitonga Bay from the 18th to the 20th centuries, or changes in the socio-economic nature of hunting practices through time. For example, the absence of carnivores during the Historical period may be explained by evolving social factors. Leónce Aubé (Aubé, 1857) documented that native animals in Babitonga Bay were classified into two groups by local communities in the 19th century: game species, consisting of animals hunted for their nutritional value; and "ferrous" animals (e.g. carnivores such as *Panthera onca*, jaguar), which were not hunted. Present-day Caiçara communities pursue different species for their food value, as well as for their medicinal value (Hanazaki et al., 2009), and both are strongly tied to cultural traditions that can be traced back to the 16th century (Camphora, 2021).

Long-term selective hunting may have had significant detrimental social and ecological consequences in the Atlantic Forest, about which our understanding remains limited (Jorge et al., 2013). Studies have shown that the selective removal of medium and large terrestrial species with low population densities, low breeding cycles, prolonged gestation periods, and extended intervals between births, not only causes a decline in the overall animal biomass, but also has far-reaching implications for forest ecosystem services (Galetti et al., 2015, 2017, 2021; Peres, 2000; Peres & Nascimento, 2006). Hunting pressure on medium and large frugivorous mammals, considered "habitat shapers" (Rumeu et al., 2020) for their capacity to disperse large seeds, may disrupt the recruitment and distribution of plant species with trophic cascade effects on plant diversity, soil regulation and structure, and forest carbon storage capacity, among others (Camargo-Sanabria et al., 2015; Galetti et al., 2015, 2017; Jorge et al., 2013; Peres, 2000; Rumeu et al., 2020; Villar et al., 2021). Moreover, native terrestrial animals play a significant role in the livelihoods of tropical and subtropical rural communities (Alves et al., 2009; Hanazaki et al., 2009; Peres & Nascimento, 2006), and their loss risks increasing the socio-ecological vulnerability of local traditional groups, and their perceptions of forest ecosystems (Milner-Gulland & Bennett, 2003; Ponta et al., 2019).

The commoditization of natural resources, coupled with significant progress in hunting, processing, and transportation technologies in recent decades, have led to unprecedented levels of defaunation in the Neotropics (Bogoni et al., 2018, 2020; Jorge et al., 2013; Peres, 2000). Our study indicates that these ecological footprints actually have deeper historical origins, which if not recognized can lead to the establishment of inappropriate sustainability targets, weak public and stakeholder support for conservation initiatives, and generational shifts in the acceptance of systems that are considered degraded (Lovell et al., 2020; McClenachan et al., 2018; Pauly, 1995; Soga & Gaston, 2018). In order to obtain a more comprehensive understanding of local animal density and its implications, further studies are needed, including studies on past faunal assemblages. Archaeological faunal remains are some of the few available sources of information on Pre-colonial and historical vertebrate diversity, and as such can shed light on the origin and changing nature of defaunation over long timescales. We recommend the integration of historical and archaeological data into modern faunal population assessments and conservation initiatives to set more informed reference baselines.

## Implications for Conservation

Influenced by a lack of historical perspective, the widespread perception of low human impact in tropical forests has led to limited conservation attention until recent decades. This historical amnesia has hindered assessments of the current environmental challenges facing the Atlantic Forest and its coastal waters, including defaunation and overfishing. A growing body of evidence indicates that the diversity of Neotropical mammals is currently under threat from various human-induced pressures, and archaeology is emerging as a key discipline for expanding our understanding of these anthropogenic pressures over long time scales. Our analysis of faunal remains from two historical sites highlights the significant role of fishing and hunting of native terrestrial wildlife during the last two centuries of human colonisation of Babitonga Bay. This study provides compelling evidence that the selective hunting of medium- and large-bodied native terrestrial mammals has persisted in the region for over 4500 years, and requires us to reconsider the idea of a heavy reliance on domestic animals during European colonisation of southern Brazil.

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## Supplemental Material

Supplemental material for this article is available online.

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