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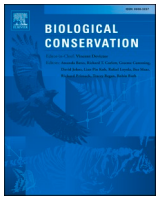

A conservation assessment of Brazil's iconic and threatened Araucaria Forest-Campos mosaic

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ABSTRACT

Southern Brazil's highland Araucaria Forest-Campos grassland mosaic is an ancient and iconic landscape in the globally important Atlantic Forest biodiversity hotspot. Human land use has inflicted significant losses on the region's natural vegetation since the late 19th Century, but these have not been effectively quantified. This study uses land cover maps and forest survey data to assess how much of the mosaic's natural vegetation remains, the quality of this remnant vegetation, how it has changed since 1985, and the extent to which it is protected.

Natural vegetation covers 13.9–37.3 % of the Araucaria Forest-Campos mosaic's core regions and 13.0–38.0 % of the whole area, depending on the dataset. Most remnant areas are degraded and remaining forests have low average integrity. In only minorities of forest plots are the landscape's characteristic *Araucaria angustifolia* trees still present (23.5 % in the Araucaria Forest region), moderately abundant (11.4 %), or >50 % of the canopy (0.5 %). Major expansions in cropland and forest plantations between 1985 and 2018 drove net/absolute losses of 12.7 %/24.1 % in the mosaic's natural forest and 38.1 %/43.2 % in its natural grasslands. Protected Areas and Indigenous Territories cover 4.6 % of the core mosaic and 6.5 % of the whole region. These conserve important remnant vegetation, though grasslands are under-protected.

By analysing and integrating diverse and complementary data sources, we significantly improve on and add nuance to previous estimates of the quantity and quality of Araucaria Forest remnants. This study also provides the first robust, quantitative estimate of remaining highland grassland across southern Brazil.

1. Introduction

South America's Atlantic Forest, also known as the Mata Atlântica (Portuguese) or Bosque Atlántico (Spanish), is one of Earth's foremost biodiversity hotspots (Myers et al., 2000). Covering over 3000 km of Brazil's coast and stretching inland to Argentina and Paraguay, half of its plant species are endemic – indeed, the Atlantic Forest's endemic species make up 2 % of all the global seed plant flora and about 3 % of the planet's mammal, bird, reptile and amphibian fauna (Brazil Flora Group, 2015; Figueiredo et al., 2021; Lughadha et al., 2016; Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000; Scheffers et al., 2019). The Atlantic Forest is also one of the world's most threatened biodiversity hotspots, with anthropogenic climate change exacerbating drastic historic habitat losses (Bellard et al., 2014; Wilson et al., 2019) – between 63 % and 96 % of the Atlantic Forest's natural vegetation has been lost (Sloan et al., 2014; MapBiomas Trinational Atlantic Forest Project). Remaining natural forest areas are highly fragmented (Ribeiro et al., 2009) and have lost between a quarter and a third of their biomass, stored forest carbon, and tree species richness (de Lima et al., 2020); almost a fifth of them are secondary forests <30 years old (Rosa et al., 2021). Pervasive defaunation, especially of large mammals, has left the Atlantic Forest "functionally 'half-empty'" (Bogoni et al., 2018, p. 17). The erosion of multiple facets of diversity, and their disproportionate impact on endemic species, is increasingly homogenising the Atlantic Forest's biodiversity (Brown et al., 2020; de Lima et al., 2020).

One of the most unique and threatened expressions of the heterogeneous Atlantic Forest is the Araucaria Forest-Campos grassland mosaic. Found on Brazil's southern highlands, this landscape occupies some of the coldest and highest-elevation niches in the Atlantic Forest and experiences high year-round rainfall (Higuchi et al., 2012; Neves et al., 2017; Uhlmann et al., 2012). The Araucaria Forest is compositionally variable but phylogenetically unique, with mixtures of typical tropical trees and more cold-adapted relicts from the Gondwanan and Andean floras (Duarte et al., 2014; Oliveira-Filho et al., 2014). Natural,

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Table 1
Summary of previous studies into the remnant natural Araucaria Forest and Campos vegetation. Studies are arranged as follows: Araucaria Forest followed by Campos; internally, by geographical extent then publication date. Entries labelled 'inferred' have been calculated using other data in the study. 'N/A' is entered where values are not provided and cannot be calculated. PR = Paraná, SC = Santa Catarina, RS = Rio Grande do Sul (states of Brazil).

Study	Methods and data sources	What is the background region? (a)	Area of background region (a)	How are the remnants described? (b)	Area of remnants (b)	% remaining (b/a)
Gantzel (1979)	Satellite imagery (Landsat II 1974–76)	Partial Araucaria Forest extent (PR, SC, RS)	15,916,855 ha	Natural forest with 50–100 % *A. angustifolia* canopy	565,419 ha	3.6 %
Gantzel (1979)	Satellite imagery (Landsat II 1974–76)	Partial Araucaria Forest extent (PR, SC, RS)	15,916,855 ha	Natural forest	2,918,727 ha	18.3 %
Sanquetta and Tetto (2000)	Field surveys (1978)	Araucaria Forest extent (PR, SC, RS)	7,379,953 ha (PR) 5,663,522 ha (SC) 4,753,623 ha (RS) 17,797,099 ha (total PR + SC + RS) (all inferred)	Primary Araucaria Forest	316,600 ha (PR) 180,100 ha (SC) 65,600 ha (RS) 562,300 ha (total PR + SC + RS)	4.29 % (PR) 3.18 % (SC) 1.38 % (RS) 3.16 % (total PR + SC + RS – inferred)
Ribeiro et al. (2009)	Satellite imagery (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2008)	Araucaria biogeographical subregion (PR, SC, RS)	25,379,316 ha	Natural forest	3,202,134 ha	12.6 %
de Lima et al. (2020)	Satellite imagery (Hansen et al., 2013)	4 × 4 km landscapes centred on Araucaria Forest plots	N/A	Forest (>70 % canopy cover)	3,840,000 ha (estimated)	17.8 % (based on plot-centred landscapes)
Marchioro et al. (2020)	Satellite imagery (MapBiomas; Souza et al., 2020)	*Araucaria angustifolia* climatically suitable area	N/A	Natural forest	N/A	42.6 % (1985) 39.3 % (2018)
Bernardinis et al. (2023)	Satellite imagery (MapBiomas; Souza et al., 2020)	*Araucaria angustifolia* climatically suitable area	48,980,000 ha	Natural forest	18,540,000 ha	37.9 % (2020)
Castella and Britez (2004)	Satellite imagery and field surveys	Araucaria Forest and Campos extent (PR)	8,295,750 ha (Araucaria Forest) 11,589,139 ha (total Araucaria Forest and Campos)	Araucaria Forest (initial to advanced succession plus Araucaria-dominated)	2,506,485 ha (Araucaria Forest) 2,741,233 ha (total Araucaria Forest and Campos)	30.2 % (Araucaria Forest) 23.7 % (total Araucaria Forest and Campos)
Castella and Britez (2004)	Satellite imagery and field surveys	Araucaria Forest and Campos extent (PR)	8,295,750 ha (Araucaria Forest) 11,589,139 há (total Araucaria Forest and Campos)	Araucaria Forest (medium or advanced succession plus Araucaria-dominated)	1,342,060 ha (Araucaria Forest) 1,436,416 ha (total Araucaria Forest and Campos)	16.2 % (Araucaria Forest) 12.4 % (total Araucaria Forest and Campos)
Vibrans et al. (2013)	Plot-based estimation and various satellite imagery	Araucaria Forest without pioneer formations (SC)	5,597,100 ha	Araucaria Forest	1,045,200-1,418,300 ha (95 % CIs, plot-based) 1,374,100-1,926,800 ha (satellite imagery)	18.7–25.3 % (95 % CIs, plot-based) 24.4–34.0 % (satellite imagery)
Vibrans et al. (2021)	Satellite imagery and field surveys	Araucaria Forest and Campos extent (SC)	5,575,304 ha	Natural forest (mid-stage secondary succession or more advanced)	1,890,629 ha	33.91 %
Overbeck et al. (2007)	Agricultural census (1996)	1970 grassland area in southern Brazil (PR, SC, RS)	18,000,000 ha	Southern Brazil's grasslands (Campos and Pampas)	13,700,000 ha	76.1 %
Overbeck et al. (2015)	Satellite imagery (MMA - Ministério do Meio Ambiente, 2007)	Potential extent of Atlantic Forest natural non-forest ecosystems (IBGE - Instituto Brasileiro de Geografia e Estatística, 2004)	11.7 % of the Atlantic Forest (12,989,340 ha inferred)	Atlantic Forest non-forest ecosystems	5.2 % of the Atlantic Forest (5,773,040 ha inferred)	44.4 %
Overbeck et al. (2015), Soares-Filho et al. (2014)	Satellite imagery (MMA - Ministério do Meio Ambiente, 2007)	Potential extent of Atlantic Forest natural non-forest ecosystems (IBGE - Instituto Brasileiro de Geografia e Estatística, 2004) (presumed)	12,989,340 ha (inferred)	Atlantic Forest non-forest ecosystems	3,339,000 ha	25.7 %
Marchioro et al. (2020)	Satellite imagery (MapBiomas; Souza et al., 2020)	*Araucaria angustifolia* climatically suitable area	N/A	Natural grassland	N/A	7.0 % (1985) 4.5 % (2018)
Bernardinis et al. (2023)	Satellite imagery (MapBiomas; Souza et al., 2020)	*Araucaria angustifolia* climatically suitable area	48,980,000 ha	Natural grassland	3,400,000	6.9 % (2020)

(*continued on next page*)

Table 1 (*continued*)

Study	Methods and data sources	What is the background region? (a)	Area of background region (a)	How are the remnants described? (b)	Area of remnants (b)	% remaining (b/a)
Castella and Britez (2004)	Satellite imagery and field surveys	Araucaria Forest and Campos extent (PR)	3,293,389 ha (Campos) 11,589,139 ha (total Araucaria Forest and Campos)	Campos (initial to advanced succession plus Araucaria-dominated)	234,748 ha (Campos) 2,741,233 ha (total Araucaria Forest and Campos)	7.1 % (Campos) 23.7 % (total Araucaria Forest and Campos)
Castella and Britez (2004)	Satellite imagery and field surveys	Araucaria Forest and Campos extent (PR)	3,293,389 ha (Campos) 11,589,139 ha (total Araucaria Forest and Campos)	Campos (medium or advanced succession plus Araucaria-dominated)	94,356 ha (Campos) 1,436,416 ha (total Araucaria Forest and Campos)	2.9 % (Campos) 12.4 % (total Araucaria Forest and Campos)
Andrade et al. (2015)	Satellite imagery (Landsat ETM+)	North-eastern plateau grasslands (RS) Central-western plateau grasslands (RS)	N/A	Highland natural grassland and associated natural forest	N/A	Northeast plateau: 41 % remnant grassland, 8 % degraded grassland, 6 % natural forest Centre-west plateau: 21 % remnant grassland, 5 % degraded grassland, 5 % natural forest

old-growth grasslands called Campos are found at the plateau's higher elevations (Andrade et al., 2019; Veldman et al., 2015). (In this study, 'Campos' refers to the South Brazilian Highland Grasslands and southern part of the Campos Gerais in Overbeck et al.'s (2022) classification.) Although they are ancient (some Campos areas are over 40,000 years old) and highly biodiverse (about a quarter of their flora is endemic), Campos are among Brazil's most neglected ecosystems – less studied, protected or appreciated than the forests which surround them (Behling et al., 2004; Iganci et al., 2011; Overbeck et al., 2015; Plá et al., 2020). Across much of their ranges, Araucaria Forests and Campos are alternative ecosystem stable states (Henderson et al., 2016a; Innes et al., 2013): contemporary climate conditions favour the encroachment of woody species, but this can be stymied by fire or grazing, to which Campos species are more resilient than tree seedlings (Müller et al., 2012; Oliveira and Pillar, 2005; Overbeck et al., 2018; Sühs et al., 2021, 2020). In balance, the result is a mosaic landscape with riverine gallery forests and small- to medium-sized forest patches embedded within a grassland matrix, with the two exhibiting sharp ecotonal boundaries (Matte et al., 2015; Müller et al., 2012). Both Araucaria Forest and Campos are characterised by the presence (and, in the forest canopy, dominance) of Araucaria trees (*Araucaria angustifolia* (Bertol.) Kuntze, Araucariaceae) – one of the world's most evolutionarily distinct and globally endangered trees, whose ancestors dominated South America's Cretaceous tropical forests (Carvalho et al., 2021; Forest et al., 2018).

Like much of the Atlantic Forest, the Araucaria Forest-Campos mosaic has been devastated since European arrival. From the late 19th and early 20th Centuries, persecution of Indigenous communities – who had lived among and shaped the highland landscape for thousands of years (de Oliveira Portes et al., 2018; Robinson et al., 2018) – made more land readily available for colonisation (Fernandes and Góes, 2018; Fernandes and Piovezana, 2015; Peres, 2009). Brazil's economic development, new infrastructure, technological advances, immigration from Europe, and the World Wars combined to open up and exert immense pressure on the potential timber resources in Araucaria Forests (de Carvalho and Nodari, 2010). By the late 1960s, *A. angustifolia* populations – which less than a century earlier had appeared to be nearly infinite – were practically exhausted (de Carvalho and Nodari, 2010). The species is now Critically Endangered (Thomas, 2013). The same drivers also inflicted habitat loss on Campos through the 20th Century and, with forest remnants depleted of valuable timber species, many landowners subsequently began converting grasslands to extensive crop monocultures (e.g. soybean) or plantations of exotic timber species (e.g. *Pinus, Eucalyptus*) (Nodari, 2016; Overbeck et al., 2007; Rossi and Nodari, 2012).

It is important to understand the location and extent of the mosaic's remaining natural vegetation for several reasons. Data on the relative rate and absolute amount of habitat loss are crucial for assessing conservation risks for species and ecosystems, as well as for evaluating and potentially mitigating the threats they face (Ferrer-Paris et al., 2019; Forest et al., 2018; Nic Lughadha et al., 2020). By clarifying the rarity and value of vegetation remnants, these data can also guide decisions about land-use planning, reforestation and conservation (Henderson et al., 2016a; Rezende et al., 2018). In landscapes with alternative stable states like the Araucaria Forest-Campos mosaic, data on the extent of natural forest and grassland – and particularly their changes through time – can help to monitor the encroachment of woody vegetation, and thereby the need for and/or success of management interventions (Oliveira and Pillar, 2005). And by leveraging data on remaining natural vegetation, studies forecasting the impacts of future climatic changes can examine their intersections with historical habitat losses, improving the real-world utility and conservation value of their predictions (Bernardinis et al., 2023; Marchioro et al., 2020; Tagliari et al., 2021b; Wilson et al., 2019).

However, despite their ecological and economic value, and despite the clear importance of historic habitat loss in understanding their present state and future trajectories, there is no consensus on how much natural vegetation remains in Araucaria Forests, Campos, or the mosaic they form. Existing studies have generally combined Araucaria Forest and Campos with other less relevant ecosystems, elided their unique complexities as a forest-grassland mosaic and/or been spatially limited. As a result of these factors, and because studies rarely analyse the same vegetation areas or use the same datasets, their estimates of remaining natural vegetation vary widely – by as much as an order of magnitude (Table 1).

Various valuable data products have assessed the Atlantic Forest's remnant natural vegetation (e.g. Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020; MapBiomas Trinational Atlantic Forest Project; Rezende et al., 2018), but these generally do not disaggregate their results for the region's different ecosystems. Ribeiro et al. (2009) did do this, including for the 'Araucaria biogeographical subregion', but like the early satellite imagery analysis of Gantzel (1979) (used in the IUCN Red List assessment of *A. angustifolia*; Thomas, 2013), their region's non-forest area includes naturally open Campos, inflating apparent losses of Araucaria Forest. de Lima et al. (2020) examined

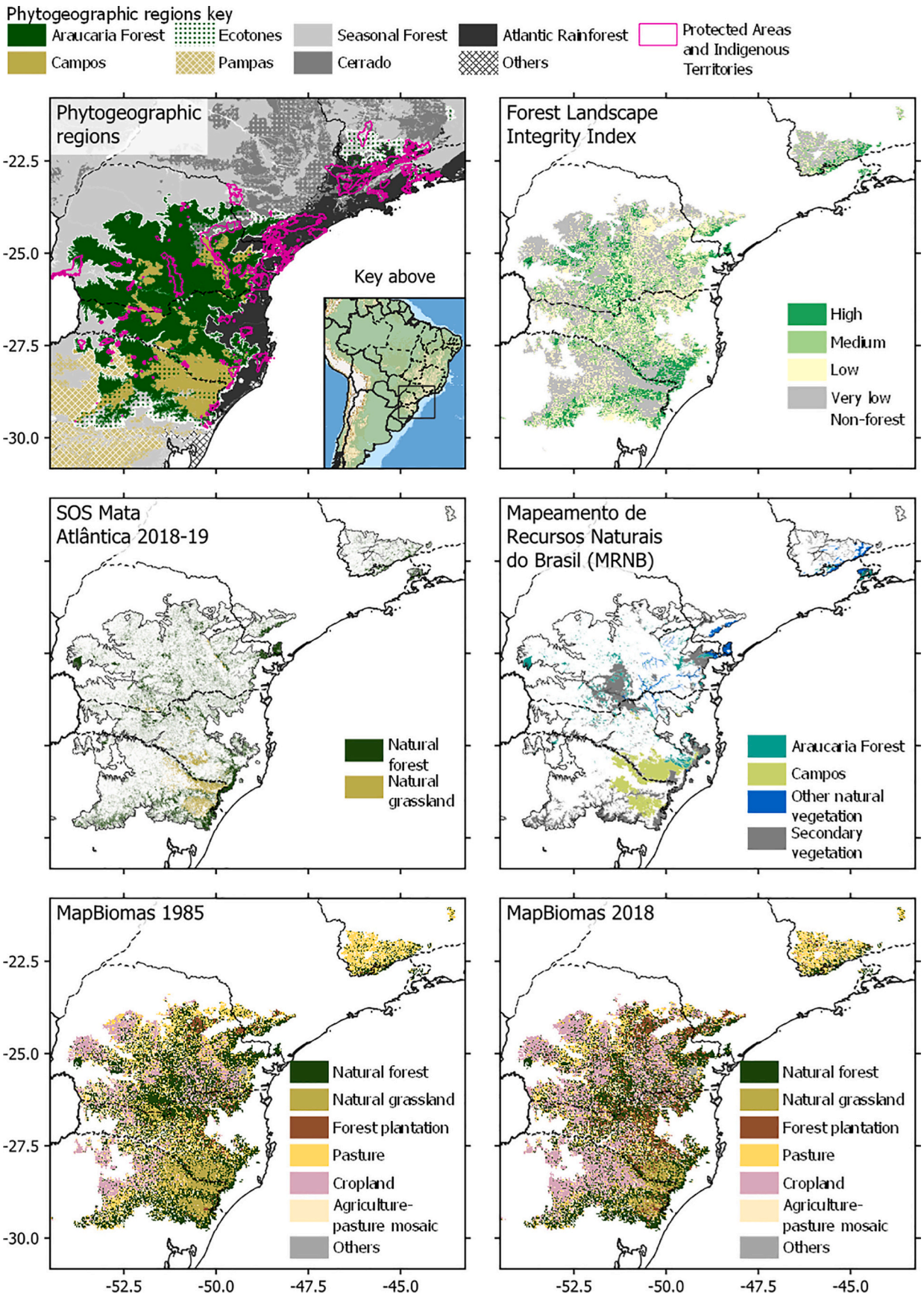

Fig. 1. Maps showing the potential and actual remnant natural vegetation on southern Brazil's highlands, according to the sources used in this study (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020; Grantham et al., 2020; IBGE - Instituto Brasileiro de Geografia e Estatística, 2018; Souza et al., 2020). The MRNB map uses tier 1 remnants (see Methods Section 2.2).

remnant forest areas in the landscapes immediately around their Araucaria Forest study plots, but it is not straightforward to generalise from these locations to the wider ecosystem. These, with Sanquetta and Tetto (2000) and Marchioro et al. (2020), are the only studies to have examined the bulk of the ecosystem's range across Paraná, Santa Catarina and Rio Grande do Sul states, and only Bernardinis et al. (2023) have examined the north-eastern areas of Araucaria Forest in São Paulo, Rio de Janeiro and Minas Gerais states. Campos have been even more neglected: the only studies to have assessed their remnant extent have combined them with Pampas (Overbeck et al., 2007) or all non-forest ecosystems in the Atlantic Forest (Overbeck et al., 2015; Soares-Filho et al., 2014), interpreted their remnant extent against an over-large background area (all climatically suitable space for *A. angustifolia*; Bernardinis et al., 2023; Marchioro et al., 2020), or examined them in detail only in Rio Grande do Sul (Andrade et al., 2015).

1.1. Aims

In light of these important knowledge gaps, this study seeks to determine: a) how much natural forest and grassland remains across Brazil's Araucaria Forest-Campos mosaic, b) the quality of those remnants, c) the changes in the mosaic's land cover over the last three decades, and d) the extent to which its contemporary natural remnants are protected. Several recent data sources, covering both satellite imagery and field surveys, are integrated in order to provide a detailed overview of the conservation state of this ancient, iconic and threatened landscape.

2. Methods

All analyses were performed using QGIS v.3.14 (QGIS Development Team, 2020) and the 'terra' package in R v.4.2 (Hijmans, 2021; R Core Team, 2020). All calculated values can be found in the Supplementary Data file.

The total area which could currently be occupied by different types of natural vegetation is assessed using the phytoecological regions in the 1:250,000-scale Mapeamento de Recursos Naturais do Brasil (MRNB) product (IBGE - Instituto Brasileiro de Geografia e Estatística, 2018–2021 version used). The MRNB data are derived from the analysis of various sources of satellite imagery and allied field work since the 1990s, and are presented in vector format at 1:250,000 scale. Although Araucaria Forests extend into north-eastern Argentina, such detailed data on their potential extent are only available for Brazil, so this study is restricted to Brazilian territory. Six regions are relevant to this study (see Figs. 1 and S1): Araucaria Forest (referred to as 'Floresta Ombrófila Mista' in MRNB, code M), Campos ('Estepe', E, within the Atlantic Forest region), their ecotonal areas with one another (EM), and Araucaria Forest's ecotones with Seasonal Forest ('Floresta Estacional', NM), Atlantic Rainforest ('Floresta Ombrófila Densa', OM), and Cerrado ('Savana', SM). We consider the mosaic's 'core regions' to be areas of Araucaria Forest, Campos and their ecotones with one another (M, E and EM; see Fig. S1). Although frequently described as 'original' or 'pre-Columbian' vegetation cover, these areas actually describe potential contemporary vegetation – the true historical coverage (e.g. at European arrival) of different vegetation types is unknown and probably did not match its current potential, as a result of Indigenous land management and/or natural, climate-induced vegetation changes (de Oliveira Portes et al., 2018; Robinson et al., 2018). It should be noted, too, that the description of vegetation areas as 'natural' does not exclude the possibility that pre-colonial Indigenous land use may have had a role in shaping their location, composition or structure (McMichael, 2021).

2.1. Remaining natural vegetation area

Several data sources were used to analyse the coverage of phytoecological regions with remnant natural vegetation: the MRNB data on contemporary vegetation (IBGE - Instituto Brasileiro de Geografia e Estatística, 2023, 2018, 2012); the 2018–19 SOS Mata Atlântica atlas of Atlantic Forest remnants (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020); and data for 2018 from collection 4.1 of the annual series of land use and land cover maps of Brazil from the MapBiomas Project (Souza et al., 2020). The MRNB data is derived from combinations of satellite imagery analysis and decades of field campaigns; although the project was completed in 2017 and updated in 2021, it does not claim to represent land cover in any single specific year. SOS Mata Atlântica is available in vector format, and derives from satellite imagery classification at 1:50,000 scale. The MapBiomas Project is a multi-institutional initiative to generate annual land use and land cover maps from automatic classification processes applied to satellite imagery; data are available in raster format at 30 m resolution. Further details on the projects can be found on their websites (https://metadadosgeo.ibge.gov.br/geonetwork_ibge/srv/por/catalog.search#/metadata/3b3c686e-8c91-41d8-94aa-dd861461f0b0/formatters/xsl-view?root=div&view=advanced, https://www.sosma.org.br/, https://mapbiomas.org/) or from the related publications (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020; IBGE - Instituto Brasileiro de Geografia e Estatística, 2023, 2012; Souza et al., 2020).

MRNB provides a hierarchical classification for each assessed parcel of land, which extends from the phytogeographical region and potential natural vegetation to current predominant and additional land cover and land use classes. It also distinguishes remnant primary vegetation from secondary natural vegetation – that is, natural vegetation which is in various stages of succession following significant recent disruption from human actions, such as mining or agriculture (IBGE - Instituto Brasileiro de Geografia e Estatística, 2012). By contrast, the MapBiomas and SOS Mata Atlântica data provides a single classification for each pixel/parcel assessed. For its forest class, MapBiomas identifies fragments larger than 0.5 ha in area without consideration for their likely quality, and therefore many of its 'natural forest' areas are recent – often only a few decades old (Rosa et al., 2021). SOS Mata Atlântica, by contrast, includes only forest fragments larger than 3 ha which appear to be more mature and have either a closed canopy or no satellite-visible evidence of degradation.

Both practically and conceptually, it can be challenging to separate natural grasslands from pasture when using remote sensing data: grazing can play an important role in Campos management so the two land cover types are not mutually exclusive, and while degradation from overgrazing can be seen in field surveys it is often impossible to detect in satellite images (Andrade et al., 2015; Müller et al., 2012; Overbeck et al., 2018; Vibrans et al., 2021). SOS Mata Atlântica's 'natural non-forest' category includes grasslands used for grazing, as does the MRNB natural grassland classification (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020). The automatic classification process of MapBiomas does distinguish the two, though they are often confused: ca. 38 % of reference areas classified as grassland in the Atlantic Forest by MapBiomas collection 4.1 were actually pasture (https://brasil.mapbiomas.org/en/estatistica-de-acuracia/colecao-4-1/, last accessed 16/01/2024).

To calculate the area of remaining natural vegetation, the vector layers (SOS Mata Atlântica and MRNB) were projected to the WGS84 UTM 22S coordinate system, clipped to the highlands' phytoecological regions, and had the areas of their constituent polygons calculated, which were then summed for each phytoecological region. For the MapBiomas raster data, the natural forest and natural grassland pixels were extracted as separate layers, the area of each pixel was calculated, and these values were summed within each phytoecological region.

2.2. Quality of remnant vegetation

The different datasets used to examine the extent of remaining natural vegetation have different thresholds on what they include (see

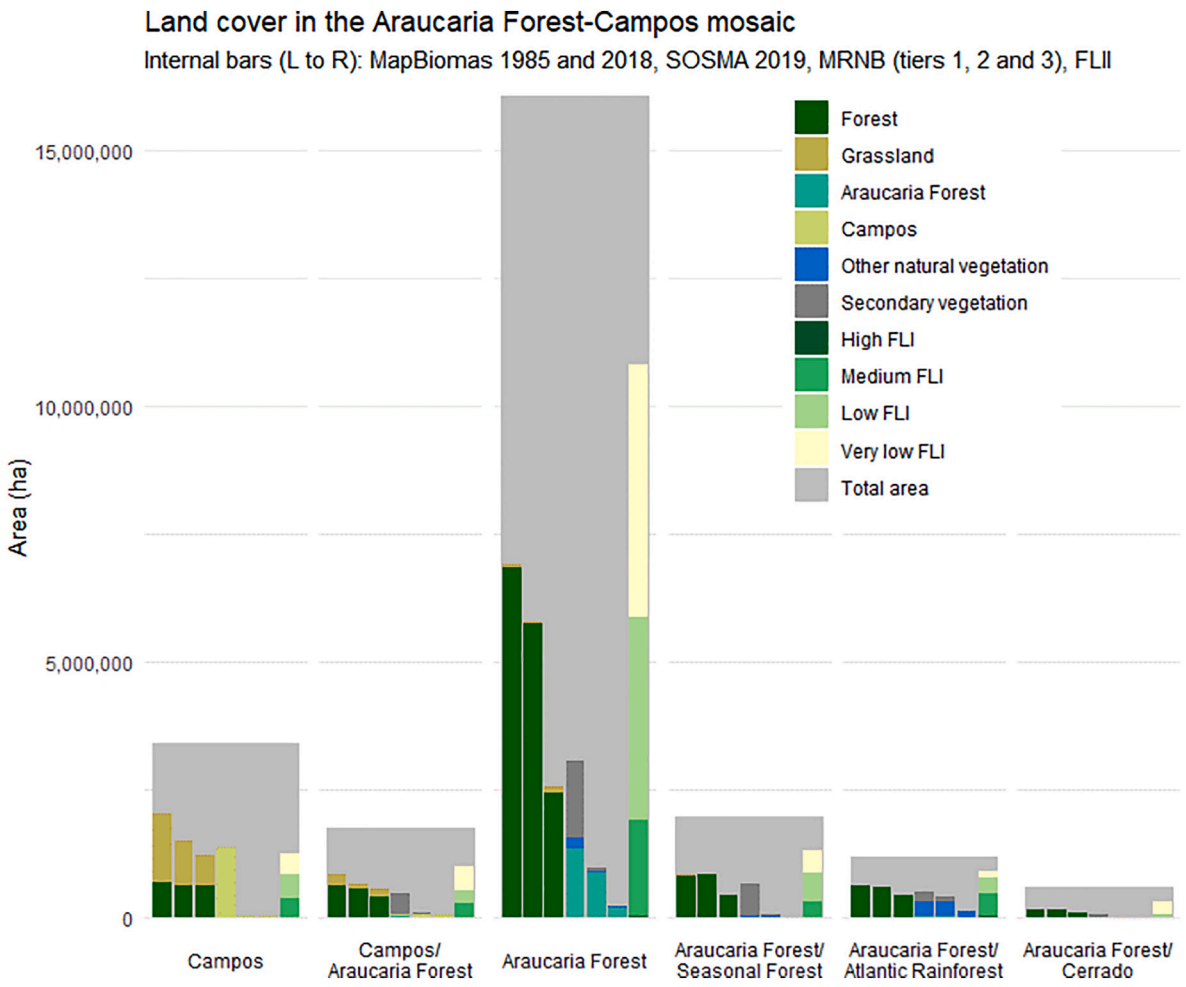

Fig. 2. The proportions of the highlands' different phytoecological regions assessed as retaining natural vegetation. Sources for the internal bars are (left to right) MapBiomas 1985 and 2018 (Souza et al., 2020), SOS Mata Atlântica (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2020), MRNB tiers 1, 2 and 3 (IBGE - Instituto Brasileiro de Geografia e Estatística, 2018), and FLII (Grantham et al., 2020). MRNB's Campos category includes gallery forests. For the data which underpin this figure, see Supplementary Data.

Section 2.1), so comparing them provides insights into remnant areas' quality. SOS Mata Atlântica and MapBiomas both use classified Landsat images but SOS Mata Atlântica has more stringent criteria for including forest fragments, so consequently these are likely to be in better condition than those mapped by MapBiomas. The hierarchical categorisation of MRNB allows areas of primary and secondary vegetation to be separated. To extend the comparison between datasets, the MRNB data were further separated into three tiers: areas which are predominantly covered by natural vegetation but which may have some anthropic land use (tier 1), areas with purely natural vegetation cover but including secondary vegetation (tier 2), and areas with purely natural vegetation cover and no secondary vegetation (tier 3). Tier 1 remnants are used in the analysis of remnant area and protection, and all three tiers are used to analyse remnant quality. For further details on the MRNB tiers, see Supplementary information.

Data from the Forest Landscape Integrity Index (FLII) complement this approach. The FLII quantifies observed and inferred human pressures on wooded areas (such as infrastructure, agriculture, tree cover loss, and their effects), as well as the loss of forest connectivity, in 300 m pixels (Grantham et al., 2020). Average FLII scores (expressed as percentages) were calculated for forest areas across the MapBiomas, SOS Mata Altântica and MRNB datasets (Supplementary information). Additionally, mean and median FLII values (as well as their standard deviation and range) were calculated within each phytoecological region, using the FLII raster projected to the WGS84 UTM 22S coordinate reference system. The area covered by vegetation with different classes of FLII was also assessed. The continuous FLII was expressed as a percentage and classified using the divisions in the index's original publication (Grantham et al., 2020), with high integrity defined as a score of >96 % and medium integrity as >60 %, and with the authors' original low-integrity class (0–60 %) split at 30 % to improve interpretation; scores <30 % are taken to be 'very low integrity'.

Data from field surveys provide an important complement to remotely sensed products like the FLII, since there are limitations to how well satellite-derived datasets can represent ecological conditions at ground level. Here, data on *A. angustifolia* trees sampled as part of Brazil's national forest inventory (NFI) were used to generate additional insights into the quality of remaining Araucaria Forest areas (data released in September 2020: https://snif.florestal.gov.br/pt-br/component/content/article/17-ultimas-noticias/717-arvores-do-brasil [last accessed 13/05/2022]). *A. angustifolia* is the ecosystem's defining species and can naturally dominate the canopy, but was also one of Brazil's most heavily exploited trees during the 20th Century and its timber remains more widely traded in Brazil than almost any other species (Brandes et al., 2020; de Carvalho and Nodari, 2010; Oliveira-Filho et al., 2014; Souza, 2021); the absence of Araucaria trees from Araucaria Forest areas could therefore be a sign of degradation.

To assess the occurrence of *A. angustifolia*, we used NFI plots which had been systematically installed on a 0.18° (ca. 20 km) grid across the states of Paraná, Santa Catarina and Rio Grande do Sul; plots installed on

Table 2
Metrics of forest remnant quality. Mean and median Forest Landscape Integrity Index values for each region; and the proportions (with 95 % confidence intervals) of plots in Brazil's National Forest Inventory of Paraná, Santa Catarina and Rio Grande do Sul in which *A. angustifolia* trees >10 cm dbh were present, covered >1 m^2/ha, or comprised >50 % of the plot's canopy.

	Campos	Campos/Araucaria Forest	Araucaria Forest	Araucaria Forest/ Seasonal Forest	Araucaria Forest/Atlantic Rainforest	Araucaria Forest/ Cerrado
Mean (median) FLII (%) – all region	42.2 % (42.8 %)	37.1 % (32.7 %)	34.0 % (33.3 %)	39.7 % (40.9 %)	57.8 % (61.6 %)	11.6 % (1.1 %)
Mean (median) FLII (%) – protected	34.9 % (32.0 %)	51.5 % (51.1 %)	53.0 % (57.4 %)	43.1 % (40.0 %)	63.8 % (69.6 %)	16.8 % (18.1 %)
N NFI plots	89	51	422	31	9	6
N with Araucaria present	23	17	99	5	0	1
% with Araucaria present (95 % CIs)	25.8 % (16.6–35.1 %)	33.3 % (20.1–46.6 %)	23.5 % (19.4–27.5 %)	16.1 % (2.6–29.6 %)	0 %	16.7 % (−22.4–55.8 %)
N with Araucaria >1 m^2/ha	9	6	48	2	0	1
% with Araucaria >1 m^2/ha (95 % CIs)	10.1 % (3.8–16.5 %)	11.8 % (2.7–20.8 %)	11.4 % (8.3–14.4 %)	6.5 % (−2.6–15.5 %))	0 %	16.7 % (−22.4–55.8 %)
N with > 50 % Araucaria canopy	0	2	2	0	0	0
% with >50 % Araucaria canopy (95 % CIs)	0 %	3.9 % (−1.5–9.4 %)	0.5 % (−0.2–1.1 %)	0 %	0 %	0 %

finer grids (most of them in Santa Catarina) were excluded, producing a grid of 571 plots within the mosaic (Vibrans et al., 2020, 2010). In an additional 19 grid locations where no plot had been installed (generally due to the absence of natural forest), we added a point with *A. angustifolia* marked as absent. We then calculated the proportion of these NFI plots in which *A. angustifolia* trees >10 cm diameter at breast height were present or moderately abundant. 95 % confidence intervals around these proportions were calculated following Vibrans et al. (2013). 'Moderate abundance' is here defined as exceeding an arbitrary cut-off of 1 m^2/ha basal area. This value is a low bar for *A. angustifolia* abundance when compared to previously published basal area values for the species: 12.1–12.8 m^2/ha (Paludo et al., 2016), 7.2 m^2/ha (range 0.2–25.6 m^2/ha; Orellana and Vanclay, 2018), and ca. 8.8 m^2/ha (35.8 % of 24.5 m^2/ha; Souza, 2007; Vibrans et al., 2020, 2011). Low estimates of Araucaria presence and/or abundance could result from forest loss, degradation, natural processes (such as NFI plot locations in areas where *A. angustifolia* would not be expected), or combinations thereof.

The dominance of *A. angustifolia* trees was also examined by determining in how many NFI plots they likely exceeded 50 % of the canopy coverage, since Gantzel (1979) assessed that such forest areas covered only 3.6 % of the area they would naturally have dominated. For this, the basal area (BA) of dominant or emergent Araucaria trees within each NFI plot was converted to potential crown area (CA; horizontal projection) following Costa et al. (2013):

$$CA = 505.6 \times BA + 5.0742$$

To exceed 50 % canopy coverage of a 4000 m^2 NFI plot, phytosocially dominant Araucaria trees would need to have a total absolute basal area in excess of 3.946 m^2. 95 % confidence intervals were calculated as above. For additional details, see Supplementary information.

2.3. Change through time

We use data from MapBiomas to examine changes in the region's land cover over the last several decades. MapBiomas rasters for 1985 and 2018 were masked to the outer limits of the highlands' phytoecological regions (i.e. not subdivided between them), projected to WGS84 UTM 22S, and cross-tabulated to demonstrate how pixels from each class had changed from 1985 to 2018. Rarer land cover types were combined into the 'other' class: savanna, wetlands, other non-forest formations, sugar cane, urban area, other non-vegetated areas, rocky outcrop, mining, and river/lake/ocean.

2.4. Protection of remnant vegetation

To assess the extent to which the Araucaria Forest-Campos mosaic's natural vegetation is protected, the locations of Brazil's legal Protected Areas and Indigenous Territories (Terras Indígenas) were downloaded from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2022) and FUNAI (http://geoserver.funai.gov.br:80/geoserver/Funai/ows?service=WFS&version=1.0.0&request=GetFeature&typeName=Funai:ti_sirgas&outputFormat=SHAPE-ZIP, accessed 26/5/2022). Data from MapBiomas, SOS Mata Atlântica, MRNB and FLII were clipped to these areas, and the land cover analyses above repeated. The NFI analyses were not reapplied since relatively few plots were located on protected land, and the MapBiomas time-series analysis was not conducted for these areas because only a small proportion of the highlands' Protected Areas and Indigenous Territories were in place before 1985.

3. Results

3.1. Remaining natural vegetation area

Southern Brazil's highland vegetation regions cover 24,921,995 ha in total – 16,048,776 ha of Araucaria Forest, 3,390,085 ha of Campos, 1,751,104 of ecotonal areas between the two, and 3,732,029 ha of Araucaria Forest's ecotones with other formations. In each region, according to all three sources evaluated (MRNB tier 1, SOS Mata Atlântica and MapBiomas), natural vegetation now covers less than half of the total area (Fig. 2).

The three different sources are all broadly in agreement regarding the proportion of the Campos region which is currently covered by natural grasslands and their embedded gallery forests and woodland patches. This stands at 35.4–44.0 %, though a large proportion (40.6–51.8 %) of this is forest rather than grassland in MapBiomas and SOS Mata Atlântica. MRNB uses a single category of grassland with gallery forest in this region (termed 'Campos' in Fig. 2 and Supplementary Data). The sources' estimation of natural vegetation in Campos/Araucaria Forest ecotones is similarly consistent (26.1–36.2 %), though MRNB suggests the great majority (87.0 %) of this is secondary vegetation, and again MapBiomas and SOS Mata Atlântica record much more of this as forest (71.8–87.0 % of the total) rather than grassland.

The three sources are much less consistent in their estimation of the Araucaria Forest region's remnant natural vegetation: 36.0 % according to MapBiomas; 16.0 % according to SOS Mata Atlântica; and 8.3 % Araucaria Forest, 1.3 % other natural (pioneer or refugial) vegetation, and 9.5 % secondary vegetation according to MRNB (tier 1). A similar pattern arises in Araucaria Forest's ecotonal areas with Seasonal Forests:

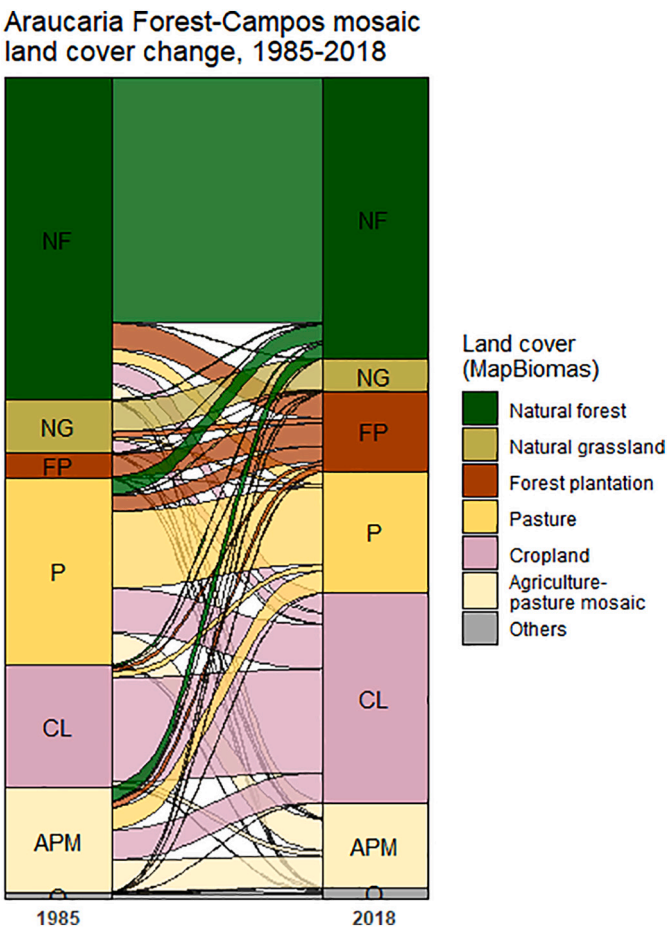

Fig. 3. Alluvial plot showing how the highlands' natural vegetation in 1985 changed by 2018, according to MapBiomas data. Some changes may result from classification changes rather than genuine land cover transitions. Data underpinning this figure can be found in Supplementary Data.

42.5 % remnant natural vegetation from MapBiomas, 21.3 % from SOS Mata Atlântica, and 32.5 % from MRNB tier 1, of which 99.3 % is secondary vegetation. The three sources estimate that 36.6–49.9 % of Araucaria Forests' ecotones with Atlantic Rainforest are covered with natural vegetation – the highest proportion in the highlands – but only 2.5 % of this is Araucaria Forest in MRNB tier 1. The most damaged part of the highlands landscape is the region where Araucaria Forest and Cerrado meet – only 7.5–25.1 % retains natural vegetation, 99.2 % of which is secondary vegetation according to the tier 1 MRNB data.

3.2. Quality of remnant vegetation

Due to pervasive human pressures and losses of connectivity, the FLII assesses remaining forest landscapes to have low average integrity (34.0–57.8 %) in all regions – very low (11.6 %) in Araucaria Forest/Cerrado ecotones (Table 2). Refining the MRNB data from predominantly (tier 1) to purely natural areas (tiers 2 and 3) increases remnants' average integrity (Supplementary information), but drastically reduces estimates of their coverage (Fig. 2, Supplementary Data). Human impacts are evident in almost all predominantly natural Campos areas – MRNB tiers 2 and 3 record only 0.4 % natural vegetation coverage in the Campos region and 2.9–4.6 % in the Campos/Araucaria Forest region, depending on whether secondary vegetation is included. In the Araucaria Forest region, tier 1's estimates of natural, non-secondary vegetation (9.6 %) halve to 5.5 % in tier 2, and reduce further to 1.3 % in tier 3. In Araucaria Forest's ecotones with Seasonal Forest, only 1.9 % of the region has any natural vegetation in tier 2 (88.7 % of it secondary regrowth), and Araucaria Forest-Cerrado ecotones have only 0.06 % coverage of tier 2 natural vegetation; neither region has any tier 3 natural vegetation. MRNB tier 3 suggests only 9.9 % of the Araucaria Forest/Atlantic Rainforest area retains minimally disturbed natural vegetation. This proportion is far higher than in the highlands' other phytoecological regions, but its Araucaria Forest areas have lower average integrity than the region's other, more widespread, natural vegetation types (Supplementary information).

Remnant quality can be further assessed using NFI plot data (Table 2). Araucaria trees were present in 25.8 % of all NFI plots in Campos, and 33.3 % of those in Campos/Araucaria Forest ecotones. This is a relatively high proportion, considering much of this ecotonal area lacks natural vegetation (Fig. 1) and large parts of the remnants would naturally not be forest. In the Araucaria Forest region, 23.5 % of samples recorded Araucaria trees, but in only 11.4 % of the total did their total basal area exceed 1 m^2/ha. There are no established *A. angustifolia* trees in NFI plots within the Araucaria Forest/Atlantic Rainforest ecotone, aligning with the MRNB assessment that this area is better characterised by Atlantic Rainforest and secondary vegetation rather than Araucaria Forest. Across the whole southern highlands, Araucaria trees make up at least half of the canopy cover in only four of the 608 NFI plots.

3.3. Change through time

Data from MapBiomas illustrate how the vegetation on southern Brazil's highlands has changed in the last three decades (1985–2018, Figs. 2 and 3). Natural vegetation coverage in Araucaria Forests' ecotones with Cerrado, Seasonal Forest and Atlantic Rainforest changed comparatively little in this timeframe, respectively declining by 6.3 % and 1.6 %, and increasing by 1.4 %. However, the Araucaria Forest, Campos, and Araucaria Forest-Campos ecotone regions respectively had 16.4 %, 26.0 %, and 23.1 % less natural vegetation in 2018 than in 1985. In the latter two cases, losses fell more heavily on natural grasslands (declining 34.4 % in Campos and 60.2 % in Campos/Araucaria Forest) than on remnant forests (declines of 9.1 % and 10.6 %, respectively).

Across the whole highland region, there were 8,458,496 ha of natural forest in 2018, a reduction of 12.7 % from 1985's 9,689,701 ha. This headline figure, however, masks the fact that only 7,355,193 ha (87.0 %) of 2018's natural forest had been classified as such in 1985 – most of the new areas had previously been pasture or a mosaic of agricultural and pastoral land (Fig. 3). Taken together, 24.1 % of the highlands' 1985 natural forest area had been transformed by 2018. By contrast, 2018's natural grasslands were older overall (91.7 % had been present in 1985), but saw even steeper reductions in coverage, from 1,628,642 ha to 1,008,290 ha – a reduction of 38.1 %. These losses of remnant forest and grassland were driven predominantly by significant expansions in cropland (from 3,676,480 ha to 6,334,914 ha, a 72.3 % increase) and forest plantations (from 726,947 ha to 2,382,307 ha, a 227.7 % increase) – changes which also affected the distribution of anthropogenic land cover (Fig. 3).

3.4. Protection of remnant vegetation

Protected Areas and Indigenous Territories are responsible for sheltering many of the remaining significant patches of high-quality Araucaria Forest and Campos vegetation (Fig. 4). The integrity of protected forest areas is higher than the regional averages (Table 2), and currently protected areas generally have higher proportions of natural vegetation cover than the highlands more widely (Supplementary Data). Yet, overall, Protected Areas and Indigenous Territories cover relatively little of the Araucaria Forest-Campos mosaic (Fig. 5, Supplementary Data) – 5.1 % of Campos, 4.6 % of Araucaria Forest, and 3.2 % of their ecotonal area. Araucaria Forests' ecotones with Seasonal Forest and Cerrado are also poorly covered (3.1 % and 7.0 %, respectively), though 45.8 % of the Araucaria Forest/Atlantic Rainforest area is protected. Natural forest is better protected than grassland in each phytoecological region, and

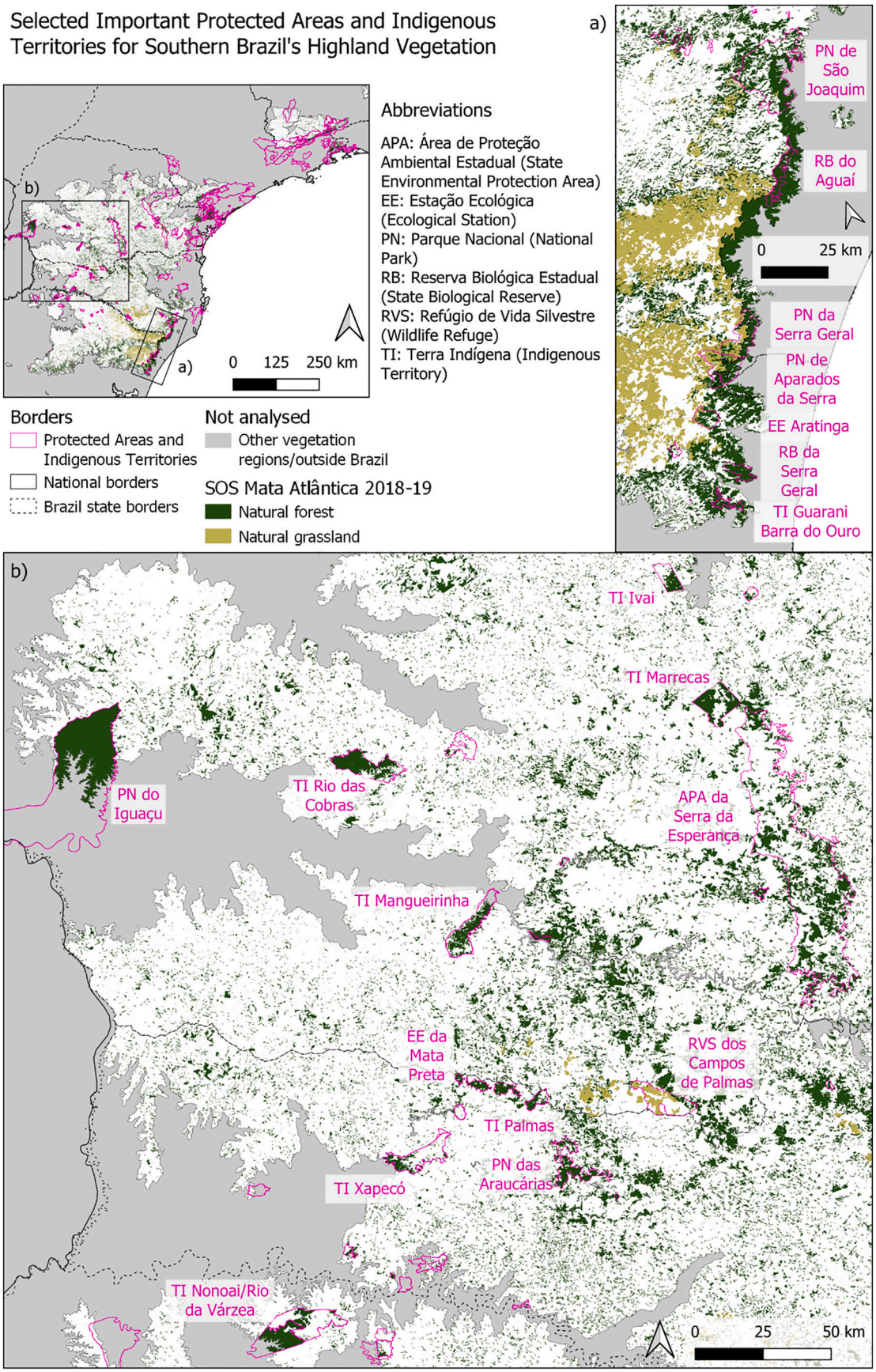

Fig. 4. Maps illustrating the contributions of Protected Areas and Indigenous Territories to the conservation of natural vegetation cover in the Araucaria Forest-Campos mosaic. Selected areas are labelled.

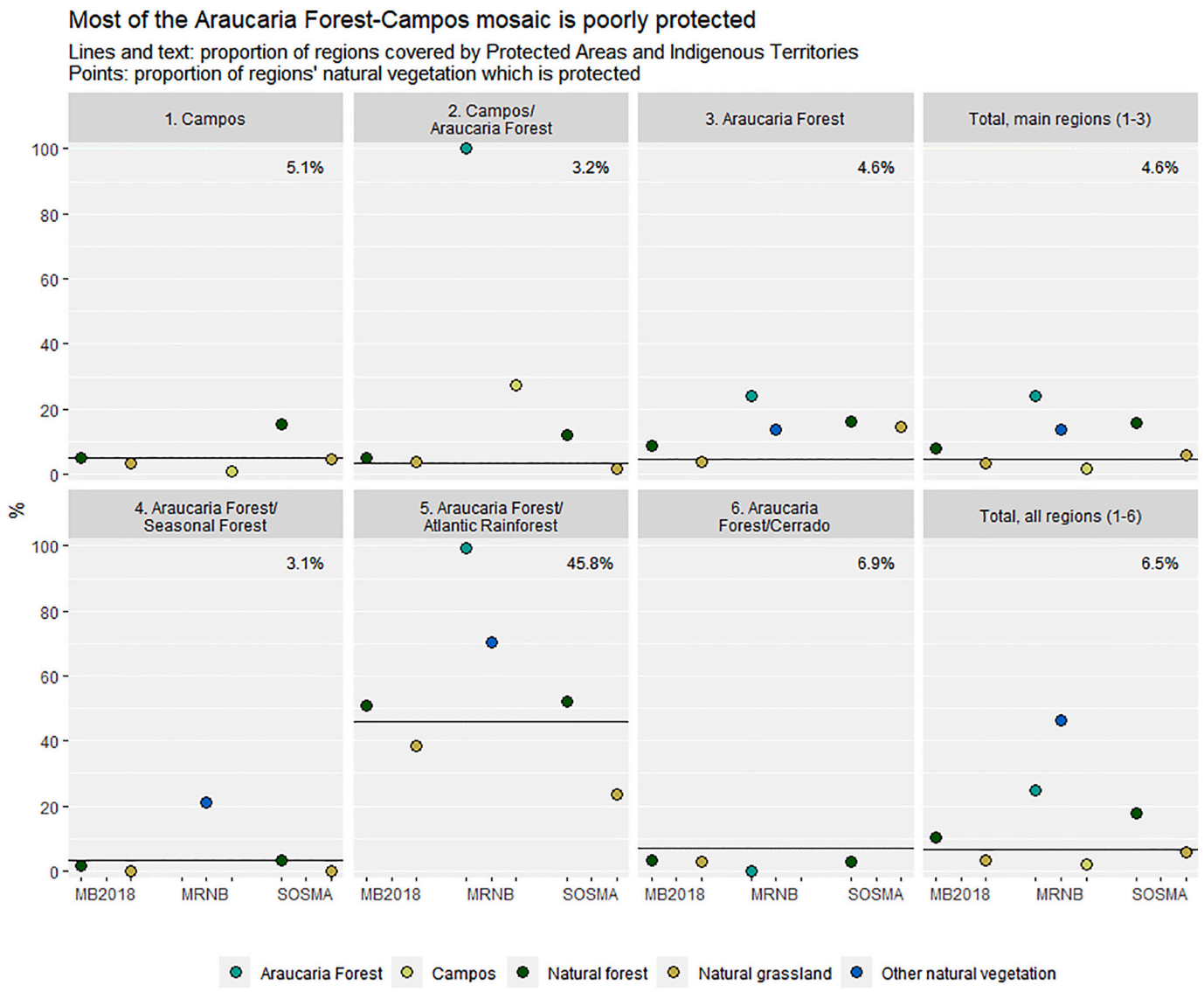

Fig. 5. The proportion of the highlands' phytoecological regions (text and horizontal lines) and remnant natural vegetation (points) covered by Protected Areas and Indigenous Territories.

the Campos region's natural vegetation remnants – especially its grasslands – are under-protected (Figs. 4 and 5).

4. Discussion

This study set out to examine four questions: how much of the Araucaria Forest-Campos mosaic's natural vegetation remains, what is the condition of the remnants, how has their coverage changed over the last three decades, and how well protected is what is left? The answers can be summarised briefly thus: little of the mosaic's natural vegetation remains, much of what is present is badly degraded, land use changes have caused significant (and somewhat masked) losses even since 1985, and the great majority of remnant natural vegetation is unprotected. Araucaria Forests have suffered greater total losses than Campos, but the grasslands are undergoing steeper contemporary declines and are even more poorly protected. The variety of approaches used in this study provides important insights into all elements of these questions, enabling us to reach a previously elusive regional synthesis and reconcile widely divergent existing assessments.

4.1. *Araucaria Forest*

Contemporary Araucaria Forest areas are much diminished from their pre-colonial state. Natural vegetation cover is absent from 64 to 90 % of the core Araucaria Forest region, primarily due to the intense exploitation it experienced during the early and mid-20th Century (de Carvalho and Nodari, 2010), but notable losses are still ongoing. Although natural vegetation cover declined by 16 % between 1985 and 2018 (Fig. 2, Supplementary Data), actual losses of natural forest may have been twice as high, masked by secondary regrowth on former farmland (Fig. 3). These trends have contributed to the southern highlands having some of the worst rates of forest cover loss and increasing isolation in the entire Atlantic Forest (Rosa et al., 2021). Remnant natural Araucaria Forest is also degraded: restricting remnant estimates to better-preserved areas reduces them drastically (from 36.0 % in MapBiomas 2018 to 1.3 % in MRNB tier 3), and very little of the remaining forest has high or even medium integrity (0.07 % and 11.8 %, respectively) (Fig. 2, Supplementary Data). Additionally, *Araucaria angustifolia* trees are found in only 19.4–27.5 % of NFI plots in the region, in only half of these do they exceed the modest basal area threshold of 1 m^2/ha, and in only two of 422 plots do they comprise at least half of the canopy

(Table 2). For the landscape's eponymous species, whose dominance is considered characteristic of the highland ecosystems, this indicates significant degradation (Oliveira-Filho et al., 2014; Souza, 2021). Complementary results from previous field studies have shown that many of these remnant areas also suffer diminished structural diversity and homogenised species composition, with their large trees disproportionately removed and their considerable carbon storage capacity significantly eroded (de Lima et al., 2020; Oliveira and Vibrans, 2020; Scipioni et al., 2019; Sevegnani et al., 2019; Souza, 2007).

Combining metrics of remnant area and quality allows the wide-ranging previous estimates of remaining natural Araucaria Forest (Table 1) to be reconciled. Higher estimates of remnants have been obtained by including a wider range of natural vegetation (e.g. 30.2 % of all successional stages in Paraná – Castella and Britez, 2004; 18.3 % for all natural forest – Gantzel, 1979), and lower ones from considering only well-conserved forests (16.2 % for medium- or advanced-succession forest in Paraná – Castella and Britez, 2004; 3.6 % for patches with *A. angustifolia*-dominated canopies – Gantzel, 1979). Our results show that it would be misleading, for example, to say that 36 % (MapBiomas, 2018) of pre-colonial Araucaria Forests have survived to the present day, since much of that natural vegetation has been heavily degraded and/or is recent regrowth. Neither would it be accurate to claim that Araucaria Forest only covers 1 % (MRNB tier 3 or high FLII) of its potential range, since natural forest remnants, including many in reasonable condition, are more widespread than this. The most appropriate synthesis is that natural forests of various quality cover around 19–36 % of the Araucaria Forest region, but higher quality areas cover no more than about 5 %, and exceedingly few patches – if any at all – have survived relatively unscathed from the 19th Century.

Our findings demonstrate how synthesising multiple locally, regionally and globally developed datasets from both remote sensing and fieldwork can move beyond single summary statistics to provide nuanced and granular insights into realities of natural land cover. They also highlight the importance – and difficulty – of rationally and explicitly choosing the most relevant remnant coverage value for any given purpose, and carefully communicating its meaning. These challenges are equally applicable in many other ecosystems around the world, especially landscapes with spatially complex natural vegetation coverage such as forest-grassland mosaics.

4.2. Campos grasslands

Comparisons with previous vegetation cover estimates are more difficult for Campos than for Araucaria Forest, since far fewer estimates have hitherto been made (Table 1). Our analyses show that natural vegetation covers 27.3–41.3 % of the Campos and Campos/Araucaria Forest regions in total, figures which sit between the most relevant previous estimates (25.7–44.4 % of the Atlantic Forest's non-forest ecosystems; Overbeck et al., 2015; Soares-Filho et al., 2014) and some way above the MapBiomas-derived estimates of Marchioro et al. (2020) and Bernardinis et al. (2023), which are somewhat artificially depressed by using the entirety of *A. angustifolia*'s model-predicted climatically suitable area as the background. This remnant area is also declining rapidly: its natural vegetation declined 25.2 % between 1985 and 2018, with its grassland component especially badly affected (declining by 37.8 %). Losses – both total and since 1985 – are thus greater in Campos (59–73 % and 25–38 %) than in Brazil's grassland vegetation as a whole (46 % and 20 %; Overbeck et al., 2022). Finally, it is important to note that the assessed area of remaining natural grassland is likely to be overestimated. As noted in Section 2.1, large proportions of the areas classified as 'natural grasslands' are grazed (see Section 2.1) and degraded grasslands are widespread (9–38 % of non-converted grassland remnants in Rio Grande do Sul state; Andrade et al., 2015) – a consequence of challenges such as mismanagement and invasive forage species – though this cannot be assessed effectively with remotely sensed data (Andrade et al., 2015; Overbeck et al., 2022; Vibrans et al., 2021).

Although formally assessing Campos against the IUCN Red List of Ecosystems criteria is beyond the scope of this study, the ecosystem should be considered threatened with collapse (Bland et al., 2016). Total reductions since ca. 1750 CE of 58.7 % (MapBiomas, 2018), 65.0 % (MRNB tier 1 with secondary vegetation) and 66.0 % (SOS Mata Atlântica) would all qualify for a status of Vulnerable under subcriterion A3 (≥50 %). The 72.7 % reduction from MRNB tier 1 without secondary vegetation equates to an assessment of Endangered under subcriterion A3 (≥70 %). The reductions over the 33 years covered by MapBiomas would also place Campos as Vulnerable (≥30 %) or Endangered (≥50 %) under subcriterion A1/A2b, depending on whether grassland areas alone or all natural vegetation were considered, and whether declines were extrapolated to the full 50-year assessment period. (Araucaria Forests have previously been assessed as Endangered under the same criteria (Ferrer-Paris et al., 2019), an evaluation which is supported by the data synthesised here.) Southern Brazil's highland Campos are therefore likely to be among Brazil's most threatened ecosystems, and merit significantly more conservation attention than they have received over recent decades (Overbeck et al., 2022, 2015, 2007).

4.3. Conservation implications

The threats to southern Brazil's highland Araucaria Forest-Campos mosaic have most often been combatted by legally protecting land, though these areas cover little of the highlands' landscape (4.6 % of its core regions and 6.5 % of its whole) or remaining vegetation (7.3–13.5 % in core regions and 9.5–18.2 % across all regions). Restrictions on land use change in these areas should mean that conversions to agricultural land, pasture or forest plantations pose less of a threat to protected natural forest and grassland than they historically have in the mosaic as a whole (Fig. 3), although many of the highlands' Protected Areas came into existence since 1985 and already contain large areas of converted land cover (Fig. 4, Table 2, Supplementary Data). Nevertheless, conservation-focused Protected Areas do effectively conserve Araucaria Forest cover, biodiversity and biomass, and shelter forest remnants which are closer to their fully natural state than unprotected ones (de Lima et al., 2020; Oliveira and Vibrans, 2020; Tagliari et al., 2021a), as reflected in the data in this study (Figs. 2 and 4, Table 2). The current Protected Area system is less well suited for Campos, however. Conservation in Brazil has been identified as having a bias towards forests at the expense of other ecosystems (Overbeck et al., 2015). In the Araucaria Forest-Campos mosaic, this can be seen in the underrepresentation of natural grasslands in existing reserves compared to both forests and the wider landscape (Figs. 4 and 5). Furthermore, Protected Areas' forest-focused management has often historically excluded the anthropogenic fire and grazing Campos require to stave off encroaching woody vegetation (Andrade et al., 2016, 2015; de Oliveira Portes et al., 2018; Overbeck et al., 2015, 2007).

With relatively little of the landscape under legal protection, working with local communities to protect, restore and sustainably use native vegetation beyond strict conservation areas should be an important priority (Bernardinis et al., 2023; Rezende et al., 2018). Treating the mosaic as a socio-ecological system in this way could potentially increase Araucaria Forests' resilience to future disturbances (Tagliari et al., 2023, 2021a), improve Campos management (Overbeck et al., 2015), effectively conserve *A. angustifolia* genetic diversity (Zechini et al., 2018), and incentivise the maintenance of natural vegetation cover (dos Reis et al., 2018). The potential benefits of a socio-ecological approach can be seen by analogy in the significant, if little studied, contributions of Indigenous Territories to the protection of high-quality Araucaria Forest remnants (Fig. 4) (Serviço Florestal Brasileiro, 2019). Southern Brazil's Indigenous people shaped the pre-colonial Araucaria Forest-Campos mosaic in important ways over thousands of years (de Oliveira Portes et al., 2018; Robinson et al., 2018), and their dispossession enabled the last century and a half of destructive land use, the grave effects of which are documented in this study (Fernandes and Góes,

2018; Fernandes and Piovezana, 2015; Peres, 2009). Safeguarding this ancient and iconic landscape into the future – especially as 21st-Century climate changes threaten the highlands with further loss, disruption and destabilisation (Bernardinis et al., 2023; Henderson et al., 2016b; Innes et al., 2013; Marchioro et al., 2020; Wilson et al., 2021, 2019) – is only likely to succeed with a return to similarly reciprocal, respectful and mutually beneficial relationships between people and the Araucaria Forest-Campos mosaic (Tagliari et al., 2023).

CRediT authorship contribution statement

Oliver J. Wilson: Conceptualization, Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Francis E. Mayle:** Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

Data generated in this study can be found in the Supplementary Data file. Datasets analysed in this study are all publicly available (each last accessed 7/11/2023): SOS Mata Atlântica (https://www.sosma.org.br/iniciativas/atlas-da-mata-atlantica/), MapBiomas (https://brasil.mapbiomas.org/colecoes-mapbiomas/), MRNB (https://geoftp.ibge.gov.br/informacoes_ambientais/vegetacao/vetores/escala_250_mil/versao_2021/), FLII (https://www.forestintegrity.com/download-data), NFI *Araucaria angustifolia* data (https://snif.florestal.gov.br/pt-br/component/content/article/17-ultimas-noticias/717-arvores-do-brasil), Protected Areas (https://www.protectedplanet.net/country/BRA), Indigenous Territories (http://geoserver.funai.gov.br:80/geoserver/Funai/ows?service=WFS&version=1.0.0&request=GetFeature&typeName=Funai:ti_sirgas&outputFormat=SHAPE-ZIP).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110650.

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