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Understanding Land-Use Driven Biodiversity Change: Frontiers in Linking Ecological and Socio-Economic Data and Models

Links between deforestation, conservation areas and conservation funding in major deforestation regions of South America

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Abstract

1. Land-use change is a major driver of biodiversity loss, affecting tropical forests and savannas at an unprecedented rate. To protect these ecosystems and their biodiversity, national conservation areas and international conservation funding have increased considerably in these regions. Understanding of how conservation funding allocation relates to dynamics in deforestation and conservation areas is crucial to identifying what mobilizes and distributes conservation funding.

2. By applying fixed-effect models on 30 years of dynamics in forest cover, conservation areas and conservation funding in the main deforestation regions of South America, we analysed the conservation funding allocation strategies in relation to deforestation (proactive vs. reactive), conservation areas (expanding or consolidating) and previous investment (agglomerating or not). We also assessed whether allocation strategies vary across regions and the stages of deforestation and conservation.

3. We found that funding allocation followed conservation areas and higher prior funding levels over space and over time, across all regions and deforestation stages. This highlights the important role of recognized conservation areas (including protected areas and Indigenous territories) in mobilizing financial support for conservation.

4. The allocation strategies relating to forest dynamics, however, varied depending on the scale of analysis, whether we look at the temporal or spatial dimension, and in which regions we assessed the allocation patterns. Capturing region-level biases and within-region dynamics is crucial for more effective and equitable conservation.

5. As public and private actors commit to mobilizing more conservation funding and conserving more areas of the Earth, our insights on the relations between forest change and conservation efforts can help improve the allocation of conservation areas and conservation funding.

1 | INTRODUCTION

Land-use change has been a major driver of recent biodiversity loss, particularly in tropical and subtropical forests (Jaureguiberry et al., 2022). From the 1990s to the present, an estimated 65,000 to 95,000 km^2 of tropical forests has been cleared annually, with the highest rate of forest loss observed in Latin America (Achard et al., 2014; Hansen et al., 2013; Pendrill et al., 2022). Deforestation not only leads to declines in biodiversity due to habitat loss, degradation and fragmentation (Alroy, 2017; Barlow et al., 2016; Gibson et al., 2011) but also poses threats to global and regional climates (Lawrence et al., 2022; Salazar et al., 2015), water provisioning (Spera et al., 2016; Xu et al., 2022), and other ecosystem functions (Blundo-Canto et al., 2020; Hall et al., 2022). Similarly, deforestation can lead to deprivation of access to forest-based resources, posing threats to the livelihood of forest-dependent people (Levers et al., 2021; Newton et al., 2016; Olesen et al., 2022).

As forests play a critical role in sustaining biodiversity, carbon stocks and livelihoods, combating deforestation has become a central issue for biodiversity conservation, climate mitigation and sustainable development (Oldekop et al., 2020; UN Climate Summit, 2014). Protected areas have become a central approach to combating deforestation. From the early 1990s to early 2020s, protected areas designated and recognized by national governments have increased from covering less than 10% to almost 17% of global lands and waters (UNEP-WCMC, IUCN, 2021) with most of the expansion in countries of the Global South, particularly in South America (Jenkins & Joppa, 2009). Similarly, international donors have committed an increasing amount of funding to address deforestation trends in the tropics, and more broadly to support nature conservation in the Global South, with South America being a hotspot (Kuemmerle et al., 2019; Miller et al., 2013; Reed et al., 2020). From the late 1980s to the early 2010s, the amount of international conservation funding has increased nearly tenfold and now constitutes a significant proportion of available conservation resources in many countries of the Global South (Bovarnick et al., 2010; Deutz et al., 2020; Miller et al., 2013). Along with these efforts, forests recovered in some regions but continued to shrink at varying rates in other regions (Armenteras et al., 2017; Buchadas, Baumann, et al., 2022). As the Kunming-Montreal Global Biodiversity Framework foresees mobilizing at least 200 billion US dollars per year in biodiversity-related funding by 2030

(CBD, 2022), a better understanding of how conservation funding allocation approaches the deforestation and conservation area dynamics is crucial to identify what mobilizes and distributes conservation funding.

Global-scale research, typically relying on country-level data, is not well suited to unravelling such patterns, as it masks within-country variation and hinders analysis of whether conservation efforts within a country target or avoid deforestation areas (Bare et al., 2015; European Commission, Joint Research Centre, 2021). More fine-grained research on funding, typically within single countries, has sometimes found a positive association between funding and deforestation within and near protected areas (Brockington & Scholfield, 2010; de Oliveira & Bernard, 2017; Nakamura Lam, 2017). However, it is often unclear what happens outside protected areas or before the protected areas were created. Recently developed subnational conservation funding databases offer an opportunity to simultaneously consider dynamics in deforestation, conservation areas, and conservation funding across space and over time, which could help unravel such knowledge gaps (Devkota et al., 2022; Nakamura Lam, 2017; Qin et al., 2022). Such an assessment could provide information on how conservation decisions interact with other land uses, particularly in the context of parallel increases in deforestation and conservation areas (Buchadas, Qin, et al., 2022; Zimmerer, 2011).

Drawing from land-system science and conservation science, we explore two conceptual perspectives in the context of deforestation frontiers that link conservation approaches with forest cover and conservation area dynamics (Buchadas, Qin, et al., 2022; Meyfroidt et al., 2024). The first perspective views conservation as responding to the expansion of the deforestation frontier, aiming to halt or slow its progress (Kuemmerle et al., 2019; Laako & Kauffer, 2021). From this perspective, we can describe different approaches to allocating conservation resources as proactive (e.g. securing untouched lands with high forest cover and low forest loss) or reactive (e.g. intervening in areas facing high deforestation; Brooks et al., 2006; Wilson et al., 2019). The other perspective sees conservation less as a response to deforestation frontiers but more as an advancing frontier in itself, where actors are trying to formalize land dedicated for conservation in areas that have high conservation value, notwithstanding their current level of threat (Guyot, 2011; Peluso & Lund, 2011; Ramutsindela et al., 2019). From this perspective, funding allocation may emphasize the expansion

of conservation areas or supporting the consolidation of existing conservation areas (Adams et al., 2019). In addition, funding can be agglomerating by emphasizing areas already receiving more conservation funding, where existing conservation infrastructure exists, or dispersing by filling previous funding gaps (Ahrends et al., 2011; Albers et al., 2008; Kronenburg García et al., 2022). While these two perspectives have been applied mostly separately to understand the dynamics of conservation resource allocation, applying them together to the same context may help contextualize the choice of allocation approach and effectively channel conservation funding and address deforestation at scale (Buchadas, Qin, et al., 2022).

In either perspective, the choice between proactive and reactive, or between expansion and consolidating approaches can be influenced by the perceived threat level and conservation values. Perceived conservation values are often associated with biases towards certain biomes (Hecht, 2005; Mempel & Corbera, 2021; Silveira et al., 2022). In addition, these perceptions may often vary across different deforestation stages, which we loosely define as how much forest remains and how fast it is lost (Gardner et al., 2014; Harstad, 2016), or conservation stages, which we here define as stages with different extent of already officially conserved area (Adams et al., 2019). Understanding how conservation strategies varied across regions of different biomes and these stages of deforestation and conservation remain unexplored and can provide contextualized insights for funding allocation.

An important area experiencing deforestation, the expansion of conservation areas and increased international conservation funding is the tropical deforestation frontiers in South America, particularly in countries such as Brazil, Bolivia, Paraguay and Argentina (López-Carr et al., 2022; Pacheco et al., 2021). This area mainly contains the biogeographical regions of Amazon, Caatinga, Cerrado, Atlantic Forest, Pantanal, Chiquitano and Chaco (Olson et al., 2001; Pacheco et al., 2021). Large-scale deforestation has been driven mainly by the expansion of commercial agriculture and plantation forestry (Baumann et al., 2022; Curtis et al., 2018), with varying timing and spatial patterns of deforestation (Buchadas, Baumann, et al., 2022). South America has also seen the largest growth of conservation areas (Jenkins & Joppa, 2009) compared to the rest of the world; concurrently, at least 150,000 km² of area in South America lost protection status between 1961 and 2017, primarily due to industrial-scale extraction and infrastructure, although some were later re-protected (Golden Kroner et al., 2019). Heterogeneity also exists in international conservation funding, which showed a strong emphasis on the rainforests, especially the Amazon (Qin et al., 2023; Young & Castro, 2021). By analysing the allocation of conservation funds concerning deforestation and conservation area dynamics through the two perspectives, we can evaluate how the context of targeted areas affects conservation responses to similar threats, thus addressing conservation gaps and informing on the best ways to fill them.

Here, we combined annual data on the extent of forest cover (Baumann et al., 2022; MapBiomas, 2022a, 2022b) and conservation area coverage (Conservation International & World Wildlife Fund, 2021; IUCN, UNEP-WCMC, 2016) between 1985 and 2017, together with a database on the spatial–temporal distribution of international conservation funding between 1985 and 2013 (Qin et al., 2022), to understand the interactions between forest cover, conservation areas and conservation funding, at the major South American deforestation frontiers. We used fixed-effects models with time lags to separately assess the temporal and spatial dimensions of the relationship between deforestation, conservation areas and conservation funding, and how such relationships were affected by the biomes, deforestation stage (i.e. deforestation rate and remaining forest cover) and conservation stages (the percentage of area already conserved). Specifically, we asked two research questions:

1. Which conservation funding allocation approaches related to deforestation (proactive vs. reactive), conservation area dynamics (expanding vs. consolidating) and previous conservation funding (agglomerating vs. dispersion) were observed in our study area?
2. How have the approaches to the allocation of conservation funding varied by different regions, deforestation stages and conservation stages?

2 | METHODS

2.1 | Sampling approach

We created 30×30 km² grids under the Abel South America Equal Area Projection to summarize the states and dynamics of land use (approximated by land-cover change, including deforestation), conservation areas and international conservation funding flowing into our study area. To minimize the effects of spatial autocorrelation, we sampled one out of every nine grid cells using a 90×90 km² fishnet, thus ending up with a total of 1291 grid cells of 900 km² size as the analysis units for the whole study area. Within the study area we further considered five regions associated with different biomes and different levels of conservation interests for region-level analysis: Amazon (569 grid cells), Caatinga (97 grid cells), Cerrado (248 grid cells), Atlantic Forest (143 grid cells), and Chaco and Chiquitano (171 grid cells; Figure 1). We did not include other regions (63 grid cells, including Pantanal, Beni Savanna and Uruguayan Savanna) in the region-level models due to the small sample size.

Temporally, we used four-year intervals to aggregate changes in forest cover, conservation areas and conservation funding to account for the time taken for evidence accumulation and decision-making (Benzeev et al., 2022). We used the pre-1993 condition as the baseline, as the 1992 Rio Summit marked the beginning of systematic commitments of bilateral and multilateral funding for conservation (Eichenauer & Reinsberg, 2017; Grubb et al., 2019). Therefore, our analysis considered the following periods: pre-1993, 1993–1997, 1997–2001, 2001–2005, 2005–2009, 2009–2013 and 2013–2017.
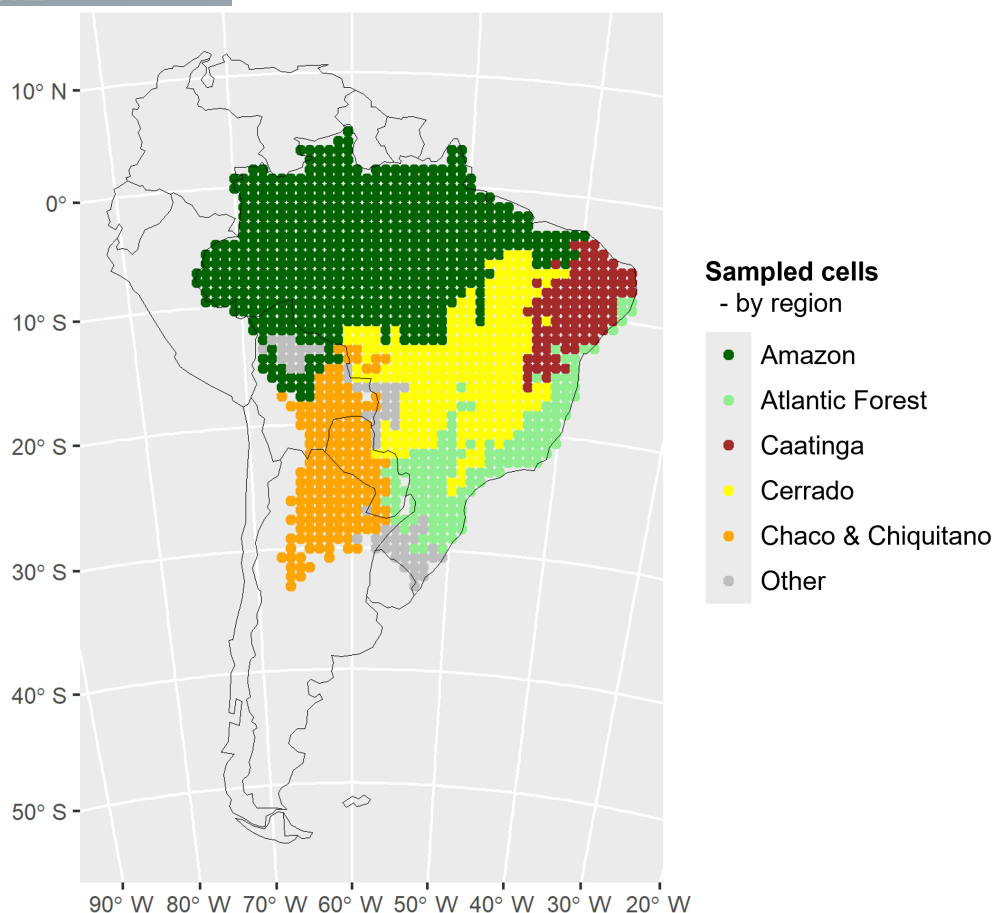
FIGURE 1 Location of grid cells used in the analyses throughout the study area and for region-level analysis.

2.2 | Data and variables

For the status and changes in forest cover, we used annual land-cover maps from 1985 to 2017 for Amazon (MapBiomas, 2022a), the rest of Brazil (MapBiomas, 2022b; Souza et al., 2020) and Chaco (Baumann et al., 2022) and reclassified the maps into forest cover versus the rest (Table S1). Using the reclassified forest/non-forest cover data, we calculated forest loss (variable=*ForestLoss*) and remaining forest cover for each 30 km × 30 km grid cell (*ForestCover*). Note that for *ForestLoss*, we only kept the positive value and adjusted the negative values (that is, gain of forest cover over time) to zero, as we assumed that more loss of forest cover could be treated as a higher level of threat, while the magnitude of gain of forest cover is less relevant in deciding the level of threat. We then rescaled the coverage and forest change to be proportional to the size of the sampling unit, ranging between 0 and 1. Within the Amazon, we also considered the cover and loss of dense forest cover only (excluding dry forests and savannas), to further test the bias towards dense rainforest in the allocation of conservation areas and conservation funding.

To capture the coverage and change of conservation areas, we relied on the World Database of Protected Areas (WDPA) and the Protected Area Downgrading, Downsizing, and Degazettement (PADDD) data (Conservation International & World Wildlife Fund, 2021). The WDPA includes protected areas as well as demarcated Indigenous territories (Terras Indígenas) in Brazil that also count towards Brazil's national commitment to the national protected area target (IUCN, UNEP-WCMC, 2018). From the WDPA records, we extracted the polygons of domestically designated areas and excluded internationally inscribed areas such as the UNESCO heritage sites, biosphere reserves, or Ramsar Convention sites. The PADDD dataset recorded known legal changes made to protected area boundaries, with relatively comprehensive geospatial record in our study area (Golden Kroner et al., 2019), which allows us to account for areas that were once under protected status but later removed (Lewis et al., 2017). Combining these two datasets, we calculated the change in protected area coverage (*ΔConsArea*) in each cell over every 4-year interval, as well as the coverage of protected areas (*ConsArea*) that existed at the end of each period. We rescaled these variables to percentages relative to the area of our cells. For simplicity, we refer to these domestically established protected areas and Indigenous territories with conservation status as *conservation areas* hereafter.

For conservation funding, we used a georeferenced international conservation funding dataset, which georeferenced more than 70% of the known amount of bilateral and multilateral conservation grants (in constant 2011 US dollars) committed to Brazil, Bolivia, Paraguay and Argentina (AidData, 2017; Qin et al., 2022; Tierney et al., 2011). To describe the spatial–temporal dynamics of international funding

allocation, we spatially allocated committed funding for each project to the project's area of interest and temporally allocated all committed funding to the year of commitment. We then calculated the total amount of funding committed to each $30 \times 30\,km^2$ cell over our four-year periods and logarithmically transformed it for our analysis (*ConsFund*). Additionally, we divided the conservation funding in each cell in each period by the total amount of funding for all the 1291 sampled cells in that period to represent the relative level of international conservation interest a cell received in that period (*ConsFund_r*). For simplicity, we refer to the committed funding of bilateral and multilateral donors as *conservation funding* hereafter.

Finally, we combined forest cover (above or below 50%) and forest loss (above or below 1%—approximately the average forest loss rate of the study area) to classify the grid cells into four deforestation stages: high forest cover low deforestation (highF-lowD), high forest cover high deforestation (highF-highD), low forest cover high deforestation (lowF-highD) and low forest cover low deforestation (lowF-lowD; Gardner et al., 2014; Figure S1). Similarly, we used conservation area coverage to categorize our samples into four conservation stages: no conservation, 0%–5% conserved, 5%–30% conserved and more than 30% conserved. More details on the categorization and the sensitivity analyses are in the Supporting Information (Figures S3 and S4).

2.3 | Statistical analyses

We used a generalized regression model framework to test the overall funding allocation approach in our study area related to the dynamics of deforestation and conservation areas (RQ1). Specifically, we tested whether higher conservation funding was allocated in areas with higher forest cover (proactive), in areas with high deforestation (reactive), and in areas with more conservation areas and previous conservation funding (agglomerating) or not (dispersing). Note that when considering where to fund conservation efforts, donors can observe and compare the status of forests and conservation areas between different locations. However, donors are unable to make the same type of comparisons across different periods, since one cannot choose among all the periods to decide which period to invest (as one cannot go back to the past or jump to the future). Therefore, the relationship between conservation funding and the dynamics of forest cover and conservation areas can vary depending on whether it is examined across different locations or different periods. To represent this difference in our model structure, we chose one-way fixed-effects models to focus separately on the time dimension and the space dimension (Kropko & Kubinec, 2020). We thus explored the assumptions mentioned above using individual fixed-effects models (to focus on the variations over time) and time fixed-effects models (to focus on the variations over space) on the panel data according

$$y_{i,t} = \alpha_i + \boldsymbol{B}\boldsymbol{X}_{i,t-1} + \varepsilon_{i,t} \tag{1}$$

$$y_{i,t} = \alpha_t + \boldsymbol{B}\boldsymbol{X}_{i,t-1} + \varepsilon_{i,t} \tag{2}$$

where, $y_{i,t}$ is the dependent variable (the logarithm of 1 plus committed conservation funding in constant US dollars, Table 1) of cell i, in the time period t; $\boldsymbol{B}$ are the effect coefficients; $\boldsymbol{X}_{i,t-1}$ is the set of independent variables related to the dynamics of the forest and the conservation area (see Table 1) of cell i, in the previous time period, $t-1$; $\varepsilon_{i,t}$ is the error term. In Equation 1, we introduced the term α_i to capture the individual fixed effect of each cell i, thus focusing on how the relationship between funding and lagged forest cover and the dynamics of the conservation area varied over time; in Equation 2, we introduced α_t to capture the fixed effect of each time step t, thus focusing on how the relationship between funding and lagged forest cover and the dynamics of the conservation area dynamics between locations.

Because the percentage of land with forest cover and the percentage of land experiencing forest loss are likely highly correlated, we also compared models with both forest cover and forest loss versus with forest loss only. For a similar concern, we tested the models with both *ConsArea* and *ΔConsArea* versus with *ΔConsArea* only as the independent variable that captures the dynamics of the conservation area. Finally, we tested whether the change in conservation areas (*ΔConsArea*) could be related to the status and changes in conservation funding and forest cover in the previous period, and whether forest loss was related to the change in conservation areas and conservation funding in the previous period. In all models, independent variables were lagged by one time step (4 years) to account for the time taken for decision-making.

To test how funding levels and approaches are affected by specific different contexts (RQ2), we applied the same model setting focusing on the spatial variation of funding (Equation 2) to the subsets of grid cells of different regions, deforestation stages and conservation stages (Table 1, Figure S1), as they are likely associated with different levels of perceived conservation value and threats that can influence the choice of conservation approach. Note that we did not analyse the temporal variation of funding (Equation 1) because the subset of grid cells in different deforestation stages and conservation stages varied in each period. For Amazon, additionally, we explored differences in using forest/deforestation metrics for all forests versus dense forests as independent variables, to explore how the observed bias towards dense forests affects the approach (Pendrill et al., 2022; Qin et al., 2022; Silveira et al., 2022). We conducted the analysis in R 4.1.0 using the R package *plm* (Croissant & Millo, 2008; R Core Team, 2021).

3 | RESULTS

3.1 | Spatial–temporal dynamics in forest cover, conservation areas and conservation funding

All five regions (Amazon, Atlantic Forest, Caatinga, Chaco and Chiquitano, Cerrado) experienced marked forest loss but deforestation varied considerably over time (Figure 2a). While the coastal Atlantic Forest, the northern Amazon and Caatinga experienced

TABLE 1 Variables used to capture the status and change of forest cover, conservation areas and conservation funding.

| Category	Variable	Description	Source
Forest cover	*ForestCover*	% of area with forest cover at the end of the period (possible range of values: 0–1)	MapBiomas (2022a, 2022b) and Baumann et al. (2022)
	ForestLoss	Loss of forest cover during the period (possible range of values: 0~1)	
	DF_stage	Deforestation stage based on the combination of ForestCover (high: >50%, low: ≤50%) and ForestLoss (high: >1%, low: ≤1%)	
State-recognized conservation areas	*ConsArea*	% of area under conservation status at the end of the period (possible range of values: 0–1)	IUCN, UNEP-WCMC (2018) and Conservation International & World Wildlife Fund (2021)
	ΔConsArea	% of area experiencing the addition or removal of the conservation area in the period (possible range of values: −1 to 1)	
	CA_stage	Conservation stage based on categorized coverage of conservation area (0, 0%–5%, 5%–30%, >30%)	
International conservation funding	*ConsFund*	(log-transformed) amount of funding committed	AidData (2017) Qin et al. (2022)
	ConsFund_r	(log-transformed) funding committed to a cell relative to the total amount of funding in the period	
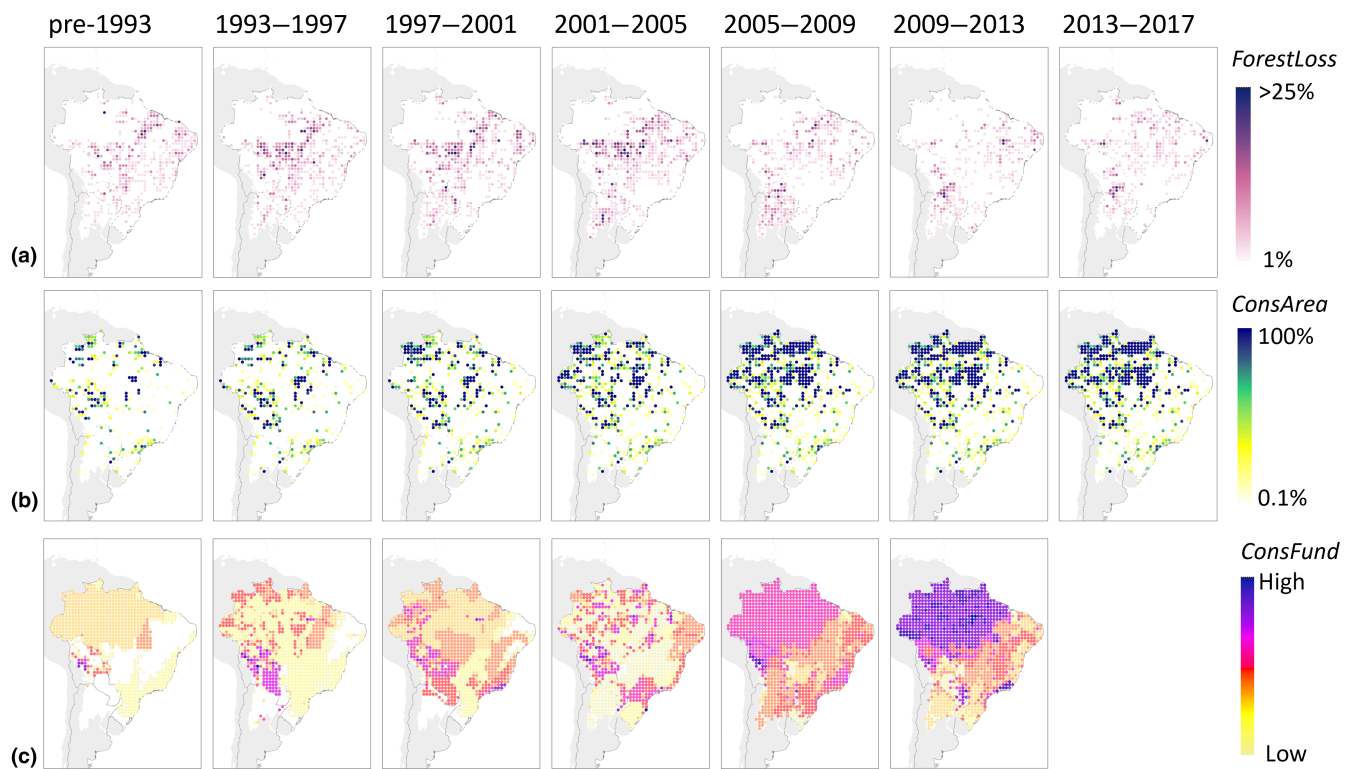
FIGURE 2 The percentage of (a) forest loss (ForestLoss), (b) conservation areas (ConsArea) and (c) the amount of conservation funding (ConsFund) at sampled $30 \times 30 \, km^2$ cells over time. Conservation funding data (ConsFund) are not available for the last period (2013–2017).

relatively less change in forest cover between 1985 and 2017, Chaco, the northern Cerrado, and the south and east of the Amazon lost substantial amounts of forest cover. Our study region also saw marked changes in conservation areas over the three decades, including significant increases in state-designated protected areas and demarcated Indigenous territories (which counted towards Brazil's national conservation targets). The strongest expansion of the conservation areas occurred in the Amazon (especially in the Brazilian part), while in other regions, the conservation areas were more scattered (Figure 2b).

In terms of the distribution of areas targeted by international conservation funding (Figure 2c, Figure S2), the western edges of the Bolivian Amazon have been the focus throughout our study period, while the Brazilian Amazon and coastal Atlantic Forest have received increasing attention since the late 1990s. International conservation interest in Paraguay has gradually shifted from the Paraguayan Chaco in the 1990s to the Paraguayan Atlantic Forest since 2000. Investment in Argentina has been much lower than in other countries. However, international conservation funding for the Argentinian Chaco has increased slightly since the 2005–2009 period.

3.2 | Relations between patterns of deforestation, conservation areas and conservation funding

When focusing on the temporal variation in conservation funding (that is, using individual fixed-effects models), we showed a clear association between deforestation dynamics and conservation funding. Specifically, we found a significant relationship between conservation funding and both forest cover and deforestation (Table 2). According to our model, conservation funding for a given period was higher when the previous period had lower forest cover (*ForestCover*) (coefficient = −3.951, $p < 0.001$) and lower levels of deforestation (*ForestLoss*) (coefficient = −3.346, $p < 0.001$). Similarly, we found a relationship between conservation funding and lagged conservation area status and dynamics. Conservation funding was generally higher when there was higher conservation area (*ConsArea*) in the previous period (coefficient = 1.249, $p < 0.001$). In the model with both the conservation area and its change as independent variables, the conservation funding was lower in subsequent periods when more conservation areas were added (*ΔConsArea*) in the previous period (coefficient = −0.471, $p < 0.001$). However, when the model included only *ΔConsArea* but not *ConsArea* as an independent

variable, we would see more funding when more conservation areas are added (that is, a higher *ΔConsArea*) (Table S2). In our study area, the interaction term of conservation areas and forest loss—as an indicator of the level of competition between conservation and other land uses that leads to deforestation—did not have a significant association with conservation funding. Models with or without *ForestCover* as an independent variable showed qualitatively similar results. The associations between conservation funding and forest cover, forest loss and conservation areas remained significant when using the detrended conservation funding measure (*Consfund_r*) as the dependent variable (Table S3).

When focusing on spatial variation in the distribution of conservation funding applying time fixed-effects models (Table 2, time fixed-effects models), the effects between funding and forest cover differed. Conservation funding tended to be higher for cells with higher forest coverage (coefficient = 0.286, $p < 0.001$) and did not have a significant association with forest loss. Higher levels of conservation funding were related to a higher coverage of conservation area (coefficient = 0.358, $p < 0.001$), but not related to lagged *ΔConsArea*. However, when excluding *ConsArea* as an independent variable, conservation funding was positively associated with lagged *ΔConsArea* (Table S2). Donors also committed more conservation funding to cells with already high interest in conservation funding in the previous period (coefficient = 0.824, $p < 0.001$). We did not find a significant relationship between conservation funding in a period and forest loss in conservation areas in the previous period, or the level of competition between conservation areas and deforestation (indicated by the interaction term between *ConsArea* and *ForestLoss*). The direction and significance level of these effects remained the same for models with or without *ForestCover* as an independent variable.

We found negligible effects of conservation funding and conservation area dynamics on the spatial variation of forest loss (Table 3).

TABLE 2 Analysing temporal and spatial variations in the distribution of conservation funding in the study area. Shown are the coefficients of four individual fixed-effects models that assess how conservation funding (*ConsFund*) relates to past forest cover and dynamics, past conservation area and dynamics, and the interaction between conservation area and forest loss.

Variables	Focus on temporal variation (individual fixed-effects models)		Focus on spatial variation (time fixed-effects models)	
	With *ForestCover*	Without *ForestCover*	With *ForestCover*	Without *ForestCover*
lag(ForestCover, 1)	−3.951***		0.286***	
lag(ForestLoss, 1)	−3.346***	−1.022**	0.103	−0.034
lag(ConsArea, 1)	1.249***	1.301***	0.358***	0.431***
lag(ΔConsArea,1)	−0.471***	−0.519***	−0.016	0.011
lag(ConsFund_r, 1)	0.163***	0.169***	0.824***	0.885***
lag(ForestLoss, 1):lag(ConsArea, 1)	−1.373	2.633	0.032	−0.518
n	1291	1291	1291	1291
t	5	5	5	5
R^2	0.206	0.113	0.260	0.236

Note: *n* indicates the number of cells included in the models and *t* indicates the number of time periods. Significance levels: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ⁺⁺$p < 0.10$.

	Focus on temporal variation fixed individual effects models	Focus on spatial variation fixed time effects
lag(ForestCover, 1)	0.224***	0.010***
	(0.011)	(0.001)
lag(ForestLoss, 1)	0.266***	0.532***
	(0.023)	(0.018)
lag(ConsArea, 1)	0.003***	−0.007***
	(0.000)	(0.001)
lag(ΔConsArea, 1)	−0.001⁺	−0.001⁺
	(0.001)	(0.001)
lag(ConsFund_r, 1)	−0.003***	−0.003***
	(0.001)	(0.001)
N	1291	1291
t	6	6
R^2	0.579	0.043

TABLE 3 Effects of the dynamics of conservation areas and conservation funding on forest loss.

Note: n indicates the number of cells included in the models and t indicates the number of time periods used in the model. Significance levels: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ⁺$p < 0.1$.

The temporal variation of forest loss was mainly associated with both previous forest loss and the remaining percentage of forest cover, while the spatial variation of forest loss was primarily related to the previous forest loss. Nevertheless, a significant (albeit small) reduction in forest loss is linked with greater conservation funding both spatially and temporally, and with greater conservation area coverage spatially.

3.3 | Comparison between different contexts

When focusing on the spatial variation of funding within different regions, a higher level of conservation funding was associated with a higher lagged conservation area coverage (Figure 3a). Lagged conservation funding was also strongly positively associated with more funding, except in the Atlantic Forest. The positive association between the level of funding and the lagged forest cover that we saw in the overall pattern (Table 2) was no longer significant for the allocation of funding within biomes, with the Cerrado being the only exception. Finally, the relationship between funding and deforestation varied markedly across different biomes. In Atlantic Forest, more funding went to grid cells with higher lagged forest loss, while in the Amazon, more funding was associated with lower lagged forest loss. However, if we use the loss of dense forests only (i.e. excluding dry forests and open forests), the preference towards lower forest loss disappeared (Table S4).

Contrary to what we expected, the funding allocation approach in different stages of deforestation and conservation areas turned out to be consistent with the results of the entire study area that a higher funding level is associated with more lagged conservation funding, more lagged conservation areas and more lagged forest cover, and has no significant connections with forest loss (Figure 3b,c). The only notable exception is the low forest cover high

deforestation stage, in which grid cells with more conservation areas did not receive more conservation funding (Figure 3b).

4 | DISCUSSION

We linked the spatial and temporal dynamics of forest cover, conservation areas and conservation funding to examine the overall approach to allocating conservation funding in South America's major deforestation frontiers, and evaluated how different biomes, deforestation stages and conservation stages are associated with different funding allocation approaches. The results showed that, in general, funding allocation was primarily proactive, consolidating and agglomerating. In other words: more funding was associated with more conservation areas and a higher prior funding level, both spatially and temporally, and with more forest cover spatially. Funding did not react to deforestation spatially but decreased temporally after periods of greater deforestation. These tendencies to prioritize areas with high forest cover, high conservation area and high previous funding were consistent at different stages of conservation or deforestation but varied across biomes. The variation in the levels of conservation funding and allocation approaches in different biomes indicates the important role of perceived value and threats at the biome level in influencing conservation approaches. Below we dive into the details and implications of the three major insights from our results: (1) the scale dependence of the proactive versus reactive conservation discussion, (2) the critical role of conservation areas and previous investment in mobilizing and channelling funding, and (3) the influence of biome-level perceptions of conservation value and threat on the choice of funding allocation strategies.

First, our results underscore the scale-dependent nature of the proactive versus reactive conservation approach discussion. At the
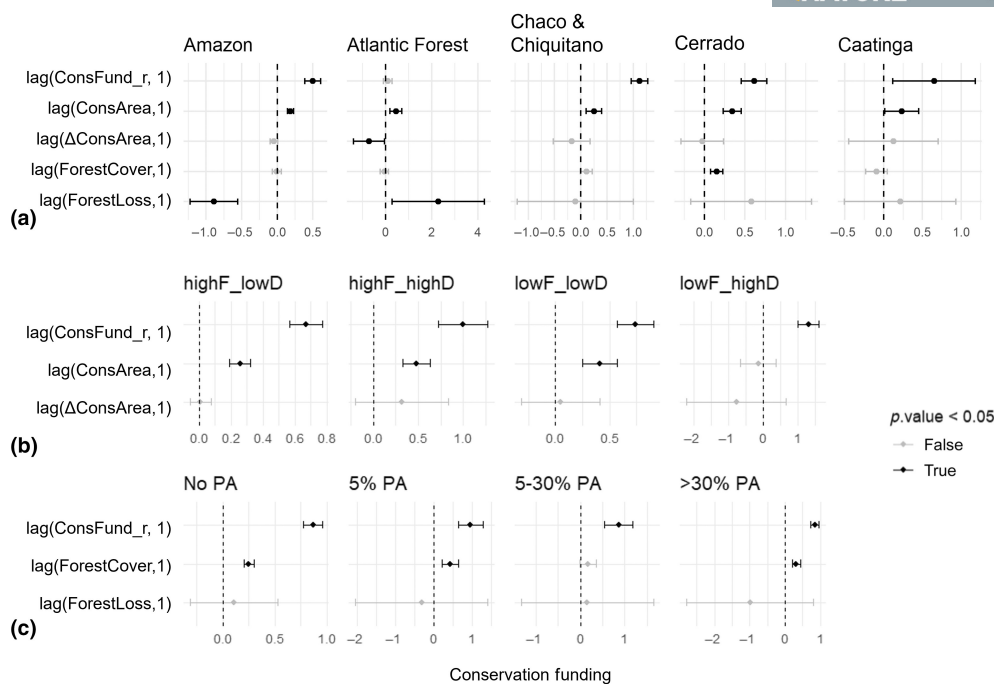
FIGURE 3 Spatial variations in the distribution of conservation funding. Shown are the coefficients of time fixed-effects models that assess how conservation funding (ConsFund) relates to funding, forest cover and dynamics, and conservation area and dynamics of a gridcell in the pevious period, in different (a) biomes, (b) deforestation stages and (c) conservation stages.

national level and the protected area level, analyses of international conservation funding showed that countries or PAs with high deforestation tend to receive more funds (Miller et al., 2013; Nakamura Lam, 2017; Reed et al., 2020). However, our subnational-level panel data found no association between spatial distribution of funding and deforestation rates. This discrepancy suggests that while global conservation responses to deforestation are robust, they may not translate to finer resolutions, potentially due to them being selectively applied across the different regions we analysed. The differences in terms of how funding responds to deforestation between scales may explain the lack of impact of international conservation investment on national deforestation rates (Bare et al., 2015). Furthermore, the proactive pattern of allocating funding to areas with more forest cover disappeared when examining the allocation strategy within each region. This suggests that the perception of international donors on conservation values and threats associated with biomes rather than fine-scale dynamics, or within biomes they may rely on alternative indicators besides forest cover.

By further separating the influence of deforestation dynamics on the spatial versus temporal variations in conservation funding, we provide a starting point for reconciling two seemingly contradicting narratives. On the one hand, conservation is often thought to prioritize intact ecosystems and avoid already highly threatened areas; on the other, conservation efforts can be expected to increase as the ecosystems of concern become more threatened (Brannstrom, 2009; Brooks et al., 2006; Harstad, 2016). Our results suggested that both perceptions can be true, as, spatially, donors committed more funding to sites with more remaining forest coverage, while over time, funding increased as forest cover decreased,

possibly as the stake of losing the remaining habitat would become higher (Armsworth, 2018; Harstad, 2016). However, since the additional funding in the next time step remained focused on areas with more forest cover instead of areas facing a high risk of deforestation, the funding allocation would over time become more focused on areas with remaining high forest cover, which aligns with the pattern we observed in the study area (Figure 2c).

Second, the strong and consistent association we observed between conservation funding and conservation areas and previous allocation of funding also indicates the usefulness of analysing conservation as a frontier itself as much as a response to other landuse frontiers (Buchadas, Qin, et al., 2022; Guyot, 2011; Laako & Kauffer, 2022). Importantly, such a pattern is consistently observed in every biome we analysed and in all stages of deforestation, except for the one with low forest cover and high deforestation. This highlights the importance of recognized area-based conservation (including Indigenous territories) in mobilizing and channelling international funding to reduce deforestation at both national and subnational levels, in most biomes, conservation stages and deforestation stages (Bhola et al., 2021; Lessmann et al., 2021; Qin et al., 2024).

The only exception to this pattern is the low forest cover high deforestation stage, in which conservation areas were not attracting more funding than non-conserved areas, possibly due to an overall lack of area-based conservation. Yet, low forest cover and high deforestation areas often also face resistance to commodity-centric conservation measures (Gardner et al., 2014; Levy et al., 2024; Oliveira & Hecht, 2016). A closer look at the very existence of different conservation interventions and their effectiveness in relation to their funding level in low forest cover and high deforestation context

will be the key to halting deforestation effectively and efficiently (Negret et al., 2024; Zhang et al., 2023).

Third, we contributed to the literature on biome-level conservation biases by showing that major deforestation regions associated with different biomes not only received varying levels of funding but also experienced different funding allocation approaches within each region (Bastos Lima & Kmoch, 2021; Qin et al., 2023; Silveira et al., 2022). However, while both the Amazon and Atlantic Forest are the focus of international conservation and have received high conservation funding as expected (Machado et al., 2020; Mempel & Bidone, 2022), in the Atlantic Forest, we see a more reactive approach that targets areas with high level of deforestation, while in the Amazon we see a more proactive approach emphasizing areas with lower deforestation. This pattern is consistent with the distinct history of the two regions. Colonial settlement and large-scale economic activities (including ranching, agricultural plantations and mining) in the Atlantic Forest have reduced its original forest cover to a mere 8% (Solórzano et al., 2021). In contrast, large-scale human migration and settlement in the Amazon began after the 1970s following infrastructure projects, leaving the biome largely intact when international concerns for biodiversity conservation in the region began to emerge (Colombo & Joly, 2010; Hecht et al., 2021). Similarly, despite all being viewed as experiencing high commodity-driven deforestation and less conservation attention (Brannstrom, 2009; Levy et al., 2024; Oliveira & Hecht, 2016), funding allocation approach in the Cerrado emphasized forest cover, while funding in Caatinga, Chaco and Chiquitano showed no significant association with forest cover. It could be that compared to increased interest in the Cerrado since the early 2000s (Colli et al., 2020), the Chaco and Caatinga were at an initial stage of attracting conservation attention (Fonseca et al., 2017; Nori et al., 2016; Oliveira-Dalland et al., 2022; Romero-Muñoz et al., 2021), and international conservation funding targeted to Chaco and Chiquitano has historically been low and sparse to specifically target any forest dynamics (Boletta et al., 2006; Zak et al., 2004). That said, while biome-level awareness disparity can explain the differences in amount of funding, other factors such as perceived conservation priorities, domestic policies, land-use actors and governance systems might better explain the differences in funding allocation approaches and are worth further exploration (Guerrero et al., 2013; Le Polain De Waroux et al., 2021; Pratzer et al., 2024).

A closer look at the Amazon shows that, unlike the loss of all forests, a higher loss of dense forests did not lead to lower conservation funding (Table S4), suggesting that comparable higher conservation attention to these forests may encourage conservation donors to be 'bolder' and not shy away from the most threatened areas. Such a contrast suggests that forest bias in conservation goes beyond biome-level disparity (Overbeck et al., 2015; Silveira et al., 2022). Even within the Amazon, the highly threatened drier and open forests have been comparably underappreciated by international conservation funding (Carvalho et al., 2019; de Carvalho & Mustin, 2017), a trend that is concerning and requires more attention from future conservation efforts.

Finally, while we did not observe any slowing down of forest loss when larger areas were protected, we did find that more conservation funding and conservation areas were associated with negligible but significantly lower levels of forest loss in space (Table 3). One possible explanation of this contrasting finding is that areas becoming formally conserved might have already been under some form of de facto conservation (e.g. Indigenous People's lands, concessions for non-timber forest products; Soares et al., 2021). In that case, formal protection might not introduce additional avoided deforestation, but they could maintain these areas in the face of growing threats. Another possible explanation is that despite the slowing down of forest loss since the establishment of conservation areas, many conservation areas tend to have very low deforestation risk due to site selection bias (Baldi et al., 2017; Ford et al., 2020; Kim & Anand, 2021). The association (or lack thereof) we found here is concerning and calls for robust impact evaluation of newly established conservation areas using outcomes and placement of additional conservation areas in sites where they can be impactful (Ghoddousi et al., 2022; Pressey et al., 2021).

Our results should be interpreted with several limitations in mind. First, this study considered only the allocation of international conservation funding, and it remains unclear whether it followed the distribution of domestic conservation funding or filled the gap. Second, since funding would in many cases flow to research, management, capacity building and consultation, rather than just to on-the-ground activities (Buxton et al., 2020), higher conservation funding values in this research should be interpreted as a relatively higher general interest of donors (and more potential resources), rather than representing a quantitative assessment of the monetary flows reaching these cells at the given period. Third, while we addressed deforestation as a major threat to biodiversity, there are other threats (for example, poaching, pollution and mining). Thus, in principle, the funding interests may not be related only to deforestation. That said, to the best of our knowledge, these other threats are not commonly targeted by conservation donors in our study area (Qin et al., 2022). Third, although we focus on the relationship between forests, conservation areas and conservation funding, other factors could affect the timing and allocation of conservation areas and funding, such as cost, governance, policies and other private sector interventions (Benzeev et al., 2022; Heilmayr et al., 2020; Holmes et al., 2012; Larson et al., 2016). Similarly, deforestation can be affected (much more) by other factors beyond conservation (Perz et al., 2008; Piketty et al., 2015). Future research to embed the conservation-deforestation interaction in broader land systems dynamics of all land-uses actors and activities will help contextualize and explain different funding allocation approaches and their effectiveness.

5 | CONCLUSION

Deforestation, conservation areas and conservation funding have grown in major ways in the last decades. A better understanding of whether they have targeted or avoided one another is crucial

to identifying what mobilizes and distributes conservation funding and their effectiveness. We found that recognized conservation areas (including Indigenous territories) are a major mechanism to mobilize and channel international conservation funding, which emphasizes the importance of maintaining existing conservation areas and recognizing other forms of area-based conservation. We also showed opposite spatial and temporal patterns in the association of conservation funding and forest cover, which can reconcile the two at first glance contradicting common perceptions on how conservation interacts with deforestation. Furthermore, funding allocation approaches varied significantly across different biomes, even for those with similar levels of conservation attention, highlighting the need for more context-specific characterization of conservation status, challenges and needs. Given the ongoing challenges of deforestation and the ambitious goals set for conservation, our analyses of the context-specific relationship between deforestation, conservation areas and conservation funding can help identify risks and opportunities to sustain forests and biodiversity.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The forest cover and conservation area data used in this study are openly available at the cited sources. The processed dataset used for the analysis is available at https://doi.org/10.5281/zenodo.13327563.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distribution and change of deforestation stages (using 50% forest cover and 1% forest loss as thresholds) over time.

Figure S2. The dynamics of international conservation funding allocation over time.

Figure S3. Spatial variations in the distribution of conservation funding using different thresholds for the four deforestation stages.

Figure S4. Spatial variations in the distribution of conservation funding using different thresholds for the four deforestation stages.

Table S1. Reclassification of land-cover data of MapBiomass to forest and dense forest cover data used in this study.

Table S2. Coefficients of forest and the change of conservation area on the spatial variations of conservation funding.

Table S3. Analysing temporal variations in relative conservation funding distribution across the study area.

Table S4. Coefficients of dense forest and conservation area dynamics on the spatial variations of conservation funding, in Amazon.

Table S5. Effects of the dynamics of conservation areas and conservation funding on forest loss.