Who holds Brazil's biodiversity? The pivotal role of private landholders

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Abstract

The urgency of tackling the biodiversity crisis across the tropics is clear, yet governance structures such as land tenure can act as barriers or enablers for conservation. Here, we focus on Brazil, a megadiverse country that has made major efforts to link deforestation to individual properties through self-reported environmental registries. Yet, how these efforts support biodiversity explicitly, remains unclear. We paired up-to-date, parcel-level land tenure data with newly developed biodiversity models to assess patterns of species richness and endemism across tenure categories. Protected areas and indigenous lands hold higher biodiversity than other categories (Cohen's $d > 0.8$), whereas private lands & claims have lower biodiversity on average (Cohen's $d < 0$) – although biodiversity was higher when these properties potentially overlap with protected or undesignated lands. We further linked these tenure patterns to compliance-related biodiversity risks and opportunities. The Pantanal, Pampas, and Mata-Atlântica held some of the areas at greatest risk of biodiversity loss from legal deforestation, whereas restoration potential was highest along the Amazon-Cerrado border. Effective conservation requires identifying where biodiversity is most vulnerable and which actors matter most. Explicitly integrating land tenure and regulatory compliance into existing policy frameworks is a first step towards more effective and lasting biodiversity conservation.

Introduction

Biodiversity is in decline at a global scale (IPBES, 2019). Whereas the tropics hold the highest species richness and endemism, they are also the most threatened by habitat loss due to land-use change (LUC) and associated indirect drivers such as the demand for agricultural commodities (Hoang et al., 2023). While the urgency of tackling biodiversity decline across the tropics is clear, existing governance structures can often act as barriers or enablers (Visseren-Hamakers et al., 2021). Land tenure – here defined as the governance system that establishes the rights and rules to access, use, manage, exclude, and alienate land ("property rights") – can therefore function as both an important barrier or potential governance tool for leveraging biodiversity conservation as it directly shapes how people use their land and associated natural resources (Pacheco & Meyer, 2022; Robinson et al., 2017).

To examine the role of land tenure in biodiversity conservation, this study focuses on Brazil, the most species-rich country in the world (Joly et al., 2019), and a major global deforestation hotspot (Hoang et al., 2023; Lapola et al., 2023). In Brazil, land tenure is key for understanding current patterns of land-use because the land management and distribution that were established during colonial rule through the 1970's continue to influence the way land is used and distributed today (Fearnside, 2005). Here, property rights are often ambiguous, meaning landholders may either suffer tenure insecurity (Araujo et al., 2009)– or exploit such ambiguity to stake claims on poorly regulated land (Carrero et al., 2022). Moreover, in contrast to many other tropical countries, Brazil has publicly available data on land tenure covering the vast majority of its territory (de Freitas et al., 2018). A large part of these data are compiled through the rural environmental cadaster (CAR for its Portuguese acronym, *cadastro ambiental rural*). The CAR requires rural property owners to self-declare property boundaries and serves as a mechanism for monitoring compliance with deforestation regulations (Freitas et al., 2017; Soares-Filho et al., 2014; Sparovek et al., 2019). This detailed information has enabled property-level analyses on deforestation (L'Roe et al., 2016; Pacheco & Meyer, 2022), as well as improved understanding of compliance with deforestation regulations (Stefanes et al., 2018).

Notwithstanding these deforestation-focused efforts, understanding how different land tenure categories hinder or facilitate biodiversity conservation goals remains pressing. First, emerging evidence suggests potential mismatches between forest or habitat cover and diverse biodiversity outcomes, as the conservation of habitat alone does not guarantee the persistence of species (Duffus et al., 2025; Marshall et al., 2021). This implies that environmental policies based solely on land-cover outcomes may be insufficient for achieving biodiversity-specific conservation goals beyond curbing deforestation (Azevedo et al., 2017; De Marco et al., 2023). For example, Brazil's Forest Code (FC), requires rural properties to maintain certain percentages of land under natural vegetation (from 20-80%, depending on the biome) (Soares-Filho et al., 2014). Yet, whether such strategies effectively mitigate biodiversity loss remains ambiguous (Brock et al., 2021; Vieira et al., 2018). Second, the land tenure of highly-biodiverse areas – i.e., who effectively "owns" biodiversity – remains a contentious issue (Fernández-Llamazares et al., 2024). In Brazil specifically , while protected areas and indigenous lands indeed play a substantial role for conservation (Lima et al., 2024), other land tenure categories that are often overlooked in conservation likely play an important role (i.e., private lands, unprotected public lands, or other communal lands). For example, evidence shows private properties in the Cerrado host up to 25% of threatened species ranges (De Marco et al., 2023). Improving understanding of the biodiversity contributions of different land tenure categories across Brazil therefore remains important.

Here, we pair (**Fig. 1; Tab. S2**) with biodiversity models of species richness and endemism (at approximately 1 km^2 resolution) in order to investigate and map the distribution of biodiversity across tenure categories. Moreover, to connect our findings more directly with existing environmental policies in Brazil, and building on previous research focused on carbon sequestration – we link tenure-biodiversity patterns with updated estimates of property-level compliance with Brazil's Forest Code (FC) (Rajão et al., 2020) (see **Methods**).

We fundamentally acknowledge that simplifying biodiversity down to a "countable unit", such as species richness, is imperfect as any single indicator fails to capture the multiple dimensions and meanings of biodiversity, and, consequently, the "ownership" of a public good such as biodiversity is likewise inherently limited (Díaz & Malhi, 2022; Fernández-Llamazares et al., 2024). Nevertheless, this approach allows us to identify policy-relevant insights as well as important gaps and opportunities for biodiversity conservation efforts across different regions in Brazil.

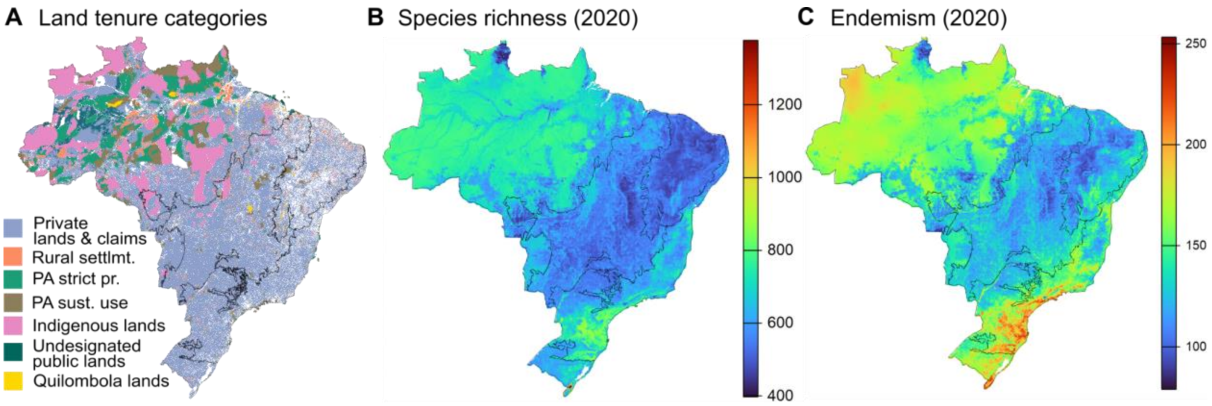

Figure 1. Land tenure and biodiversity in Brazil. (**A**) Following Pacheco & Meyer (2022), we identified the following seven categories of land tenure in Brazil: **1)** private lands & claims (*imóveis rurais*), which are privately-held rural properties and, as a result of self-declared boundaries, may or may not reflect legal titles **2)** rural settlements (*assentamentos rurais*), which are state-owned rural farmlands held by individuals or groups of families as a result of land reform (both 1-2 sourced from Imaflora (de Freitas et al., 2018)), **3)** protected areas (PA) under strict protection (*unidades de conservação de proteção integral)* **4)** PAs under sustainable use (*unidades de conservação de uso sustentável*), following definitions from the Ministry of Environment (Ministerio do Meio Ambiente, 2023), **4)** indigenous lands (FUNAI, 2023), **5)** undesignated public lands, that is, public lands under no formal designation or management (SFB, 2021), and **6)** quilombola lands, which are lands belonging to communities of escaped enslaved people and their descendants (INCRA, 2023). **(B)** Illustrates the number vertebrate, invertebrate, and plant species modeled to be found in a 1 km^2 (approximately in the year 2020). (**C**) Illustrates a per-pixel score where the number of species in (**B**), were weighed by their range, and this score was summed for all species found in a pixel. Higher numbers indicate higher numbers of endemic species. Outlines indicate Brazil's six biomes.

Methods

1. Biodiversity data & modeling

To model species richness and endemism in Brazil (**Fig 1B-C**), we compiled a variety of data sources and predicted these indicators directly as a function of key environmental variables. We opted for this approach rather than employing species distribution models because SDM-based workflows can propagate and even inflate errors from many individual species-level models, whereas modeling richness and endemism directly, by USSE approach (see below), reduces this compounding of uncertainty and allows us to explicitly incorporate effects of sampling bias (for limitations, see **Discussion** and **SM**).

We compiled species occurrence data on a broad array of taxa, covering vertebrates (birds, mammals, amphibians, reptiles), invertebrates (e.g., ants, wasps, gastropods), and plants (angiosperms and ferns) from the Global Biodiversity Information Facility (GBIF), as well as the Global Ant Biodiversity Informatics (GABI) (see **SM**). We limited the search to the global tropics and to specimen-based records to reduce taxonomic uncertainty. We removed marine records and corrected spatial inaccuracies through manual georeferencing and taxonomic validation via the Catalogue of Life (see **SM)**. This yielded a dataset of 8.6 million records of 300,228 species across the tropics of all records up to 2023. We calculated species richness and endemism using equal-area hexagonal grid cells (approximately 42 km^2), where richness was defined as the total number of species per cell, and endemism was quantified using the Corrected Weighted Endemism Index (WEIc), which assigns higher weights to species with smaller range sizes. We accounted for spatial and taxonomic sampling biases by using the Uniform Sampling from Sampling Effort (USSE) framework (U. Oliveira et al., 2024), which incorporates sampling effort into the prediction models (**SM**).

We also compiled a comprehensive suite of environmental predictors at 1 km^2 resolution, including climate (from WorldClim), topography (elevation and slope), and vegetation structure (from LIDAR and MODIS NDVI), and applied principal component analysis (PCA) to each data group to minimize collinearity (see **Tab. S1**).

Using the processed species data and environmental predictors, we trained multiple algorithms to predict species richness and endemism in 2020 on a pixel-per-pixel basis, where deep Neural Networks (DNNs) consistently outperformed other methods. Model validation was performed via five-fold cross-validation, measuring mean squared error (MSE). DNNs achieved the lowest MSE for both richness (2.79) and endemism (4.26), with R^2 values of 0.92 and 0.89, respectively (**Tab. S2**). Subsequently, we adjusted the per-pixel output values from hexagon-based predictions to 1 km^2 by dividing by a linear-scaling factor, which, albeit assumes a linear species-area relationship, allows for a conservative estimate of biodiversity metrics while keeping relative comparability across localities. Predictions were then cropped to Brazil (with endemism index values therefore based on species' tropical ranges, and respective ranges based on their occurrence records, see **SM**).

2. Land tenure data compilation & spatial overlays

Building on Pacheco & Meyer (2022), we identified and compiled several categories of land tenure in Brazil (**Fig. 1A, Tab S3**). We first cleaned any existing spatial errors, resolved self-overlaps from within categories, and identified overlapping areas across categories. These data have not undergone further hierarchization process to resolve data overlaps across different tenure categories, as this might be subject to different interpretations of how categories should be prioritized. Instead, we quantified current overlaps across categories keeping track of the precise spatial intersections across all tenure categories (see **Fig. S1** for details). Maintaining this information on potential overlaps, we conducted spatial overlays of biodiversity separately for each of these categories, following Sparovek et al. (2019).

We overlaid both gridded datasets of species richness and endemism with each land tenure data subset, extracting per-property average values in R, and plotting these distributions (**Fig. 2**). We subset observations with potential overlaps (**Fig. 3**). To statistically distinguish differences in richness or endemism among tenure categories, we used Cohen's *d* values where, Cohen's $d = \frac{mean_a - mean_b}{Standard\ deviation_{pooled}}$

Rather than solely testing for statistical significance of differences across multiple groups, Cohen's *d* values provided a standardized measure that enabled a qualitative interpretation of differences across groups irrespective of sample size. That is, Cohens *d* values answer "*how different?*" richness or endemism are across tenure categories – that is, whether there are small, medium, and large differences (**Fig. 2**)(Cumming & Finch, 2001).

3. Linking compliance with Brazil's FC to current conservation & potential restoration efforts

Brazil's FC legally requires rural properties to maintain a certain percentage of land under natural vegetation (80% in the Amazon biome, 35% in the Cerrado portions of the legal Amazon, and 20% in remaining biomes, see **SM**). Already-deforested properties are required to restore vegetation cover to comply with these percentages. According to these requirements, properties may either be in vegetation "deficit" or "surplus" to legally comply with the FC.

Building on Rajão et al.'s carbon-based estimations (2020), we used updated estimates of per-pixel vegetation surplus and deficit to 1) quantify the vegetation surplus and deficit across smallholder and largeholder private lands & claims as well as rural settlements (**Fig. 4A**), 2) identify current biodiversity conservation of the areas with "surplus" (i.e., those where deforestation could still legally occur, **Fig. 4B**), and 3) the potential for the properties with deficit to contribute to biodiversity restoration (**Fig. 4C**).

To this end, in order to compare current biodiversity patterns with potential restoration patterns, we first created a "pristine" biodiversity scenario, assuming "full" restoration, i.e., biodiversity in the absence of anthropogenic land-use (following de Marco et al., who also assume full restoration (2023))(see **SM**). To create this baseline scenario, we first modeled vegetation structure in 2020 and used this model as input in the original biodiversity models, replacing anthropogenic land-uses with the expected vegetation respective to biome classifications (e.g., tropical savannas or grasslands, tropical dry forests, etc.)(Dinerstein et al., 2017). All other environmental variables were held constant. For baseline endemism, species' range sizes were based on current distributions, but the index values reflected the predicted pristine environmental conditions. Validation of this baseline was not possible due to lack of data from entirely unaltered landscapes, however, this approach enabled comparisons between current and potential biodiversity patterns (see **SM**).

We then paired the information on the percent FC compliance with our biodiversity data. We weighed the 2020-endemism layer (**Fig. 1C**) by the percent surplus vegetation found in a given pixel (clipping only to the properties this applies to). This weighing allows for identifying which areas could potentially lose a high amount of rare species if legal deforestation were to occur (**Fig. 4B**). We then weighed the "baseline" endemism - biodiversity layer by percent vegetation deficit found in a given pixel (clipped to applicable properties). This identified the areas where complying with the FC's restoration requirements could potentially have large impacts for biodiversity (**Fig. 3C**), notwithstanding limitations (see **SM**, and **S4-5**).

Results

Biodiversity across land tenure categories

As expected, we found that potential species richness and endemism varied substantially across and within categories (**Fig. 2**). Specifically, both strict protection and sustainable-use PAs, as well as indigenous lands, had on average, higher species richness and endemism per unit – as compared to all other tenure categories (Cohen's *d* > 0.8 in these three categories for both richness and endemism: 0.78, 1.11, 1.10, for richness, and 1.10, 0.98, and 0.83 for endemism, respectively). This indicates PAs and indigenous lands indeed hold substantially higher numbers of rare species than all other categories (**Fig. 2**).

By contrast, we found that both private lands & claims as well as rural settlements had lower richness and endemism compared to all other categories (**Fig. 2**). However, Cohen's *d* values were < 0.2, indicating these differences were negligible (0.14, -0.13, for richness, and -0.12, -0.06, for endemism, respectively (confidence level 0.99)). Counterintuitively, this suggests that biodiversity in these properties can be as similar as the richness and endemism found across other categories – as the statistical difference between these is negligible. In other words, as seen in **Fig. 2**, private lands & claims as well as rural settlements are highly heterogeneous; more so than other tenure categories (**Fig. 2**).

We found small yet nuanced differences in the biodiversity found in both undesignated lands and quilombola lands as compared to other categories. First, quilombola lands had lower levels of richness and endemism as compared to PAs and indigenous lands, yet Cohen's *d* values indicate there are sufficient differences in these numbers to set quilombola lands apart from private lands & claims and rural settlements (0.34 and 0.45, for richness and endemism, respectively). Second, whereas richness in undesignated lands was substantially higher than other categories (**Fig. 2A,** Cohen's *d* = 0.83), endemism values were lower (0.29), indicating these species may not be as rare as those found in PAs or indigenous lands.

We additionally explored how consistent these findings were across Brazil's different biomes, as these represent a wide variety of ecosystems, biodiversity, and distribution of land across tenure categories. We found mostly consistent results across biomes as compared to all Brazil, (**Fig. 2; Fig. S2-S3**), with the Cerrado as a main exception. Here, we found Cohen's *d* values for endemism were substantially lower than those for species richness in rural settlements, indigenous lands, and quilombos (Cohen's *d* for richness = 0.25, 0.98, 0.73 compared to endemism = -0.07, 0.52, and 0.27, respectively) (**Fig. S2-S3, Tab. S4**). In other words, specifically in the Cerrado, the number of species was more distinct than the rarity of those species across those three tenure categories. Simultaneously, we found that endemism values in both strict and sustainable-use PAs in the Cerrado were substantially higher than for species richness (Cohen's *d* for richness = 0.56, 0.27, and endemism = 0.98, 0.53, respectively), suggesting particularly high endemism in PAs in the Cerrado (**Fig. S2-S3, Tab. S4**).

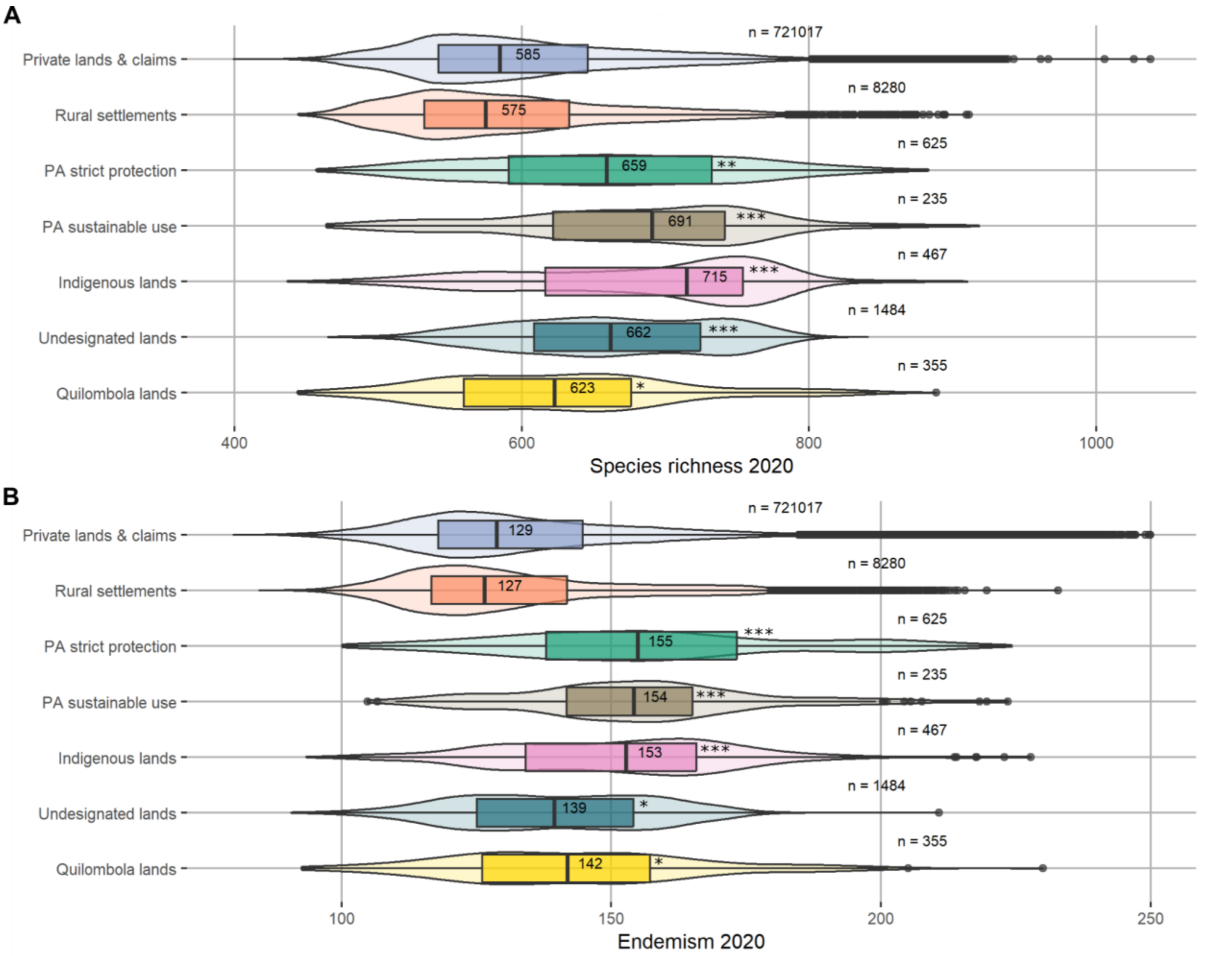

Figure 2. Biodiversity distributions across tenure categories in Brazil. Mean species richness (**A**) and endemism (**B**) are shown as boxplots (with underlying distributions shown behind as violin plots), with the median labeled on each boxplot, and *n* of each data subset is labelled to the right of each category (note, this *n* is the resulting dataset post-processing as we exclude properties <1 km^2 and does not indicate the total number of properties/units within each category). Cohen's *d* values are indicated with asterisks to show standardized differences between tenure categories, i.e., the biodiversity in one category as compared against all others (values <0.2 indicate "negligible" differences and are shown with no asterisk, <0.5 are "small" differences (*), <0.8 "medium" differences (**), and >0.8 are "large" differences (***) (confidence level 0.99)).

Additionally, given the heterogeneity of biodiversity found across private lands & claims as well as rural settlements, we specifically tested for particular biodiversity patterns in properties that have been registered as overlapping with protected areas or undesignated lands (albeit these overlaps do not necessarily indicate land conflicts, see **Fig. S1** for details). First, we tested whether the results from **Fig. 2** were sensitive to removing any private properties & claims or rural settlements with potentially overlapping areas and found that Cohen's *d* values for richness were indeed sensitive, and removing these decreased the average species richness found in private lands & claims (Cohen's *d* for richness decreasing from -0.14 to -0.21; **Tab. S5**). By contrast, we did not find endemism values were sensitive to removing these properties with potential overlaps, indicating similar levels of endemism in private lands & claims and other tenure categories with and without accounting for properties with potential overlaps. Second, we plotted the distribution of species richness and endemism for both private lands & claims and rural settlements with and without potentially overlapping areas, and again calculated differences among these groups again using Cohen's *d* (**Fig. 3**). We found richness and endemism were substantially higher in both categories with potential overlaps (differences were medium-to-large , with Cohen's *d* for richness >1 **Fig 3A-B**, and for endemism >0.5 **Fig 3C-D**). In other words, properties with overlapping registries in PAs or undesignated lands had substantially higher biodiversity than those without any overlaps, indicating these properties with potential overlaps are particularly relevant for biodiversity conservation.

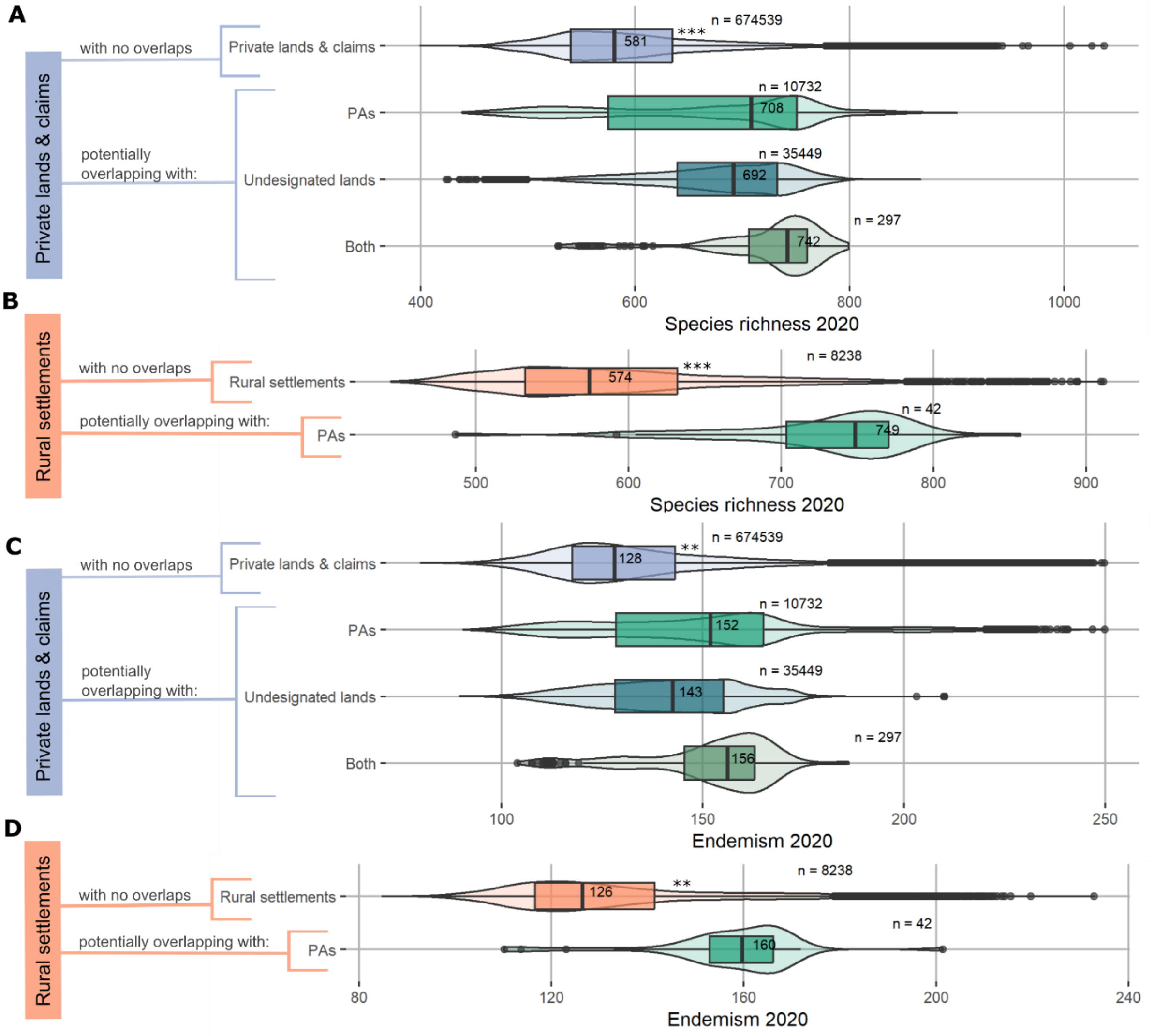

Figure 3. Species richness (**A-B**) and endemism index scores (**C-D**) in private lands & claims (**A, C**) and rural settlements (**B, D**) with and without potentially overlapping areas in protected areas, undesignated lands, or both. Similar to **Fig. 2**, the distributions of mean species richness and endemism are shown as boxplots (with underlying distributions shown behind as violin plots), with the median labeled on each boxplot, and the *n* of each data subset is labelled to the right of each category. In this case, the *n* indicates all the private properties & claims or rural settlements (respectively) with overlaps in the respective category of protected area, or undesignated lands. Cohen's *d* values are indicated with asterisks to show standardized differences between the private lands & claims/rural settlements with no overlaps, and all the observations with potential overlaps in PAs/undesignated lands. Values <0.2 indicate "negligible" differences and are shown with no asterisk, <0.5 are "small" differences (*), <0.8 "medium" differences (**), and >0.8 are "large" differences (***) (confidence level 0.99).

The role of private lands & claims for current conservation and future restoration

Previous research indicates that property size influences FC compliance (Stefanes et al., 2018) and that large properties are responsible for the vast majority of deficit (Rajão et al., 2020). Therefore, we quantified the surplus and deficit in native vegetation required for FC compliance across both private lands & claims as well as rural settlements, distinguishing between small and large landholders (defined as properties ≥ 4 fiscal modules, a Brazilian unit of measurement).

We found that out of the over 824,000 km^2 of vegetation surplus in Brazil, 82.6% of this surplus is found in largeholder private lands, with the remaining surplus found in either smallholder private lands, or in large rural settlements (**Fig. 4A**, green bar). At the same time, out of the approximately 213,000 km^2 of total deficit in natural vegetation, we found 83.5% stems from large-holding private lands (with approximately 8% owed by smallholder private lands, and another 8% by large-holding rural settlements) (**Fig. 4A**, orange bar).Hence, large private lands & claims continue to be responsible for the vast majority of FC deficit and surplus.

We found areas of surplus with high numbers of rare species across all biomes in Brazil (**Fig. 4B**), and in particular in the Pantanal and Mata Atlântica biomes, which are often not as highly prioritized as the Amazon or Cerrado. By contrast, although we also found properties with high levels of vegetation deficit and high biodiversity restoration potential throughout all Brazil (**Fig. 4C**), highest potential gains for biodiversity were along the border between the Amazon and Cerrado biomes, as well as throughout the Mata Atlântica (**Fig. 4C**, darkest areas).

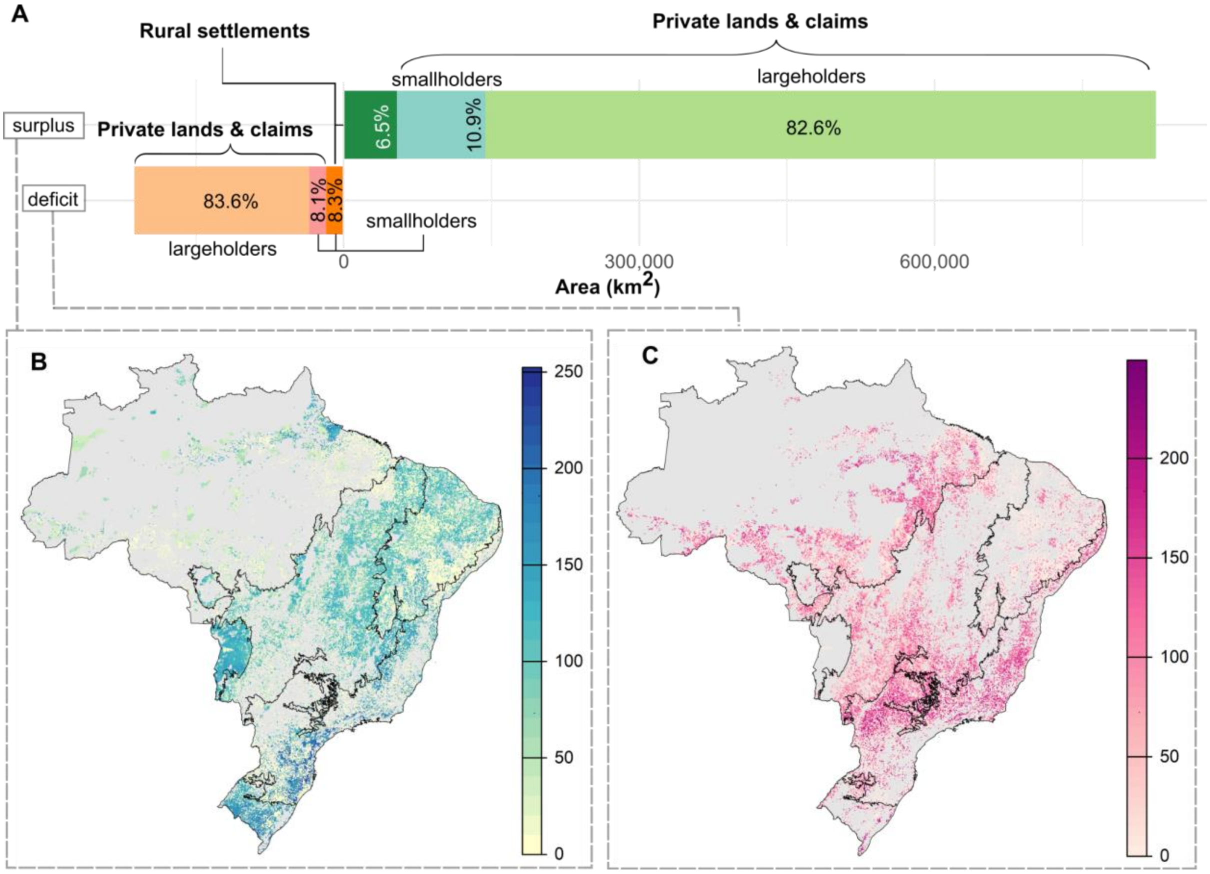

Figure 4. Total surplus and deficit in natural vegetation requirements for compliance with the Forest Code across all private lands & claims and rural settlements (≥ 1 km^2), distinguishing between small and large landholders (**A**). Note that, specifically for the category of rural settlements, only largeholder-rural settlements are visualized as having surplus (dark green bar), and only smallholder-rural settlements are visualized as having deficits (dark orange bar), as smallholders with surplus and largeholders with deficit represented >1% of the area in either category. Both **B-C** map endemism index scores weighed by the percent surplus/deficit in compliance with the FC. **B** indicates the endemism in a given pixel, weighted by the amount of vegetation surplus. Specific regions with visibly high endemism and vegetation surplus (darkest shades of blue) include: large areas of the Pantanal and Pampas, areas across Paraná and São Paulo in the Mata Atlântica, the border region between the Cerrado and Caatinga, and the island of Marajó in Pará. **C** indicates maximum potential increases in endemism through due FC compliance and biodiversity restoration. While restoration potential is

found throughout all biomes, highest potential outcomes are in the Mata Atlântica and the Amazon's border with the Cerrado (darkest shades of pink).

Discussion

We found that, on average, the tenure categories with highest species richness and endemism were both categories of protected areas and indigenous lands, notwithstanding known conservation gaps in Brazil's protected areas (Oliveira et al., 2017). This evidence supplements previous studies finding that 70% of above-ground carbon is publicly protected (Freitas et al., 2017) as well other reports that, in the Americas, species richness is higher in indigenous lands than outside (Sze et al., 2024). Although this result is reassuring, in that PAs and indigenous lands currently conserve high levels of biodiversity, evidence shows that legal protection alone may not provide sufficient or effective protection (Herrera et al., 2019). Continued support for PAs and indigenous lands remains crucial for biodiversity conservation and indigenous rights alike (Fernández-Llamazares et al., 2024; Ferrante & Fearnside, 2020). While these results confirm that areas with high levels of species richness and endemism are indeed protected, we did not specifically test for the effectiveness of these areas in conserving this biodiversity, as currently available biodiversity indicators do not allow for testing these impacts over time and such tests remain an important research frontier (Carvalho et al., 2023).

Despite finding that private lands & claims had, on average, lower levels of biodiversity than other tenure categories, our results demonstrate the complex, yet critical role of these properties in conservation and restoration efforts. Threat of agricultural expansion is highest on these lands (G. M. Oliveira et al., 2024), and in effect, we found that some private lands & claims (as well as rural settlements) with exceptionally high biodiversity were those with potentially overlapping claims in PAs and undesignated lands (**Fig. 3**). As previously mentioned, although these overlaps can only indicate *potential* conflicting land claims, this large intersection between highly biodiverse properties and potential overlaps is concerning – particularly in the Amazon, where these overlaps are primordially found (**SM**). We have previously established the key role of PAs, but undesignated lands – poorly regulated public forests that have not been designated to any particular use – are particularly vulnerable to land-grabbing and are consistently linked to deforestation (Carrero et al., 2022; Pacheco & Meyer, 2022). Thus, there is a high risk that land-clearing may be used to stake claim on these lands, as has often been the case in the past (Araujo et al., 2009; Lipscomb & Prabakaran, 2020). Based on these results, we argue that resolving these potential overlapping land claims should be a top policy priority, as others have previously and consistently argued (Azevedo-Ramos et al., 2020; Nunes et al., 2024).

A final policy implication of our findings is the prioritization of biodiversity held in properties with high levels of vegetation surplus, that is, where deforestation could still legally take place (**Fig. 4B**) – as well as properties with high levels of vegetation deficit. Previous analyses in the Cerrado indicate that if such legal deforestation were to occur, this could lead to hundreds of species' extinctions, in addition to decreases in carbon and water availability (Strassburg et al., 2017; Vieira et al., 2018). Our analysis builds upon this evidence beyond the Cerrado or Amazon – as we identify areas throughout the Pantanal, Pampas, Caatinga, and pockets of Mata Atlântica where such deforestation poses particularly high risk of biodiversity loss in largeholding private properties & claims (**Fig. 4B**). Further regulating mechanisms or incentives are needed to ensure large, private landholders throughout all biomes maintain this biodiversity in areas of FC surplus beyond what is legally required (Soares-Filho et al., 2014; van der Hoff & Rajão, 2020). Moreover, albeit compliance with restoration requirements remains low (Azevedo et al., 2017), our analysis supplements recent research highlighting the potential of targeted action (De Marco et al., 2023; Garrett et al., 2022; Stefanes et al., 2018; Vieira et al., 2018). Beyond the Cerrado, the focus of many previous studies, targeting strategies towards largeholder private lands & claims specifically along the border of Pará and Tocantins in the Amazon, in northwestern Paraná and São Paulo, and in the intersection of Espirito Santo and Bahia in Mata Atlântica could represent a first step towards more context-specific strategies that value both forest and non-forest ecosystem restoration (Brock et al., 2021). We urge policymakers to prioritize efforts targeting such landowners by implementing strategic mixes of policies and governance mechanisms, as often outlined in other research (Garrett et al., 2022).

Notwithstanding the above policy implications, our analyses are subject to several limitations related to data availability, modeling choices, and spatial scale (see **SM**). Primordially, however, we relied on a direct modeling approach that, while suitable for identifying broad biodiversity patterns across large spatial extents, does not allow inference about species-specific distributions. Incorporating species-level occurrence data, alongside improved temporal monitoring, would enable evaluations of community composition across tenure categories and represents an important research frontier.

In conclusion, as a megadiverse country with a pivotal role in global biodiversity conservation, Brazil has the opportunity to explicitly align conservation policies with biodiversity outcomes at detailed spatial scales. Many of the above suggestions confirm insights put forth by other various research in recent years, yet, these have typically been based on deforestation or other land-cover-based data (Rajão et al., 2020; Stabile et al., 2019). In sum, the continued support for PAs and indigenous lands, the resolution of conflicting lands claims, and the engagement of large private landholders across non-prioritized biomes are all urgently needed to ensure effective biodiversity conservation in Brazil. Altogether, our findings underscore how effective biodiversity conservation requires moving beyond land-cover proxies toward tenure-sensitive, biodiversity-explicit strategies.

Data and code availability

All data on the land tenure categories used in this study is publicly available. Biodiversity data are available upon request, a previous version of the forest deficit/surplus data is publicly available, and the updated version can be made available upon request. All code used for the analysis is available at https://github.com/pacheco-andrea/whoOwnsBRBD

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Supplementary materials for:

"Who holds Brazil's biodiversity? The pivotal role of private landholders"

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This appendix includes supplementary text and figures organized into the following sections:

1. Methodology for modeling biodiversity in Brazil

We directly modeled different biodiversity metrics (analogous to, e.g., Alves et al., 2020, Hortal & Lobo, 2011[1,2] , rather than following a species-distribution-modeling framework, see below, **1.1-1.6**). We carried out this modeling via the following specific steps: We first compiled and validated species distribution records from major biodiversity repositories for the tropics (**1.1**). Then, we applied the Uniform Sampling from Sampling Effort (USSE) framework[3] to these data to account for sampling bias (**1.2**). Subsequently, in preparation for these data to be used as dependent variables in the modeling, we calculated species richness and endemism using equal-area hexagons as a sampling unit (**1.3**). We also gathered a set of key environmental variables to use in the biodiversity models (**1.4**). Having compiled and preprocessed the necessary data, we carried out the biodiversity modeling by testing a diverse set of algorithms and choosing the best-performing algorithm for our chosen biodiversity metrics (**1.5**). These models thus resulted in predicted current patterns of species richness and endemism (at 1 km^2 pixels), and, while these models were initially developed for the entire tropics, we cropped these model results specifically to Brazil for this study (see implications in **1.5**). Finally, to identify areas in Brazil with high-biodiversity restoration potential (section **5**) we simulated a baseline of "pristine" biodiversity, that is, biodiversity patterns without anthropogenic-driven land-use change (LUC). We did this by first developing a model of vegetation structure (based on similar modeling techniques as described in **1.5**, as well as climate, topographic, and climatic variables) and pairing this with data on terrestrial biomes to predict hypothetical biodiversity patterns without anthropogenic LUs (**1.6**).

1.1 Sourcing and preprocessing of species distribution records

To assemble data on biodiversity distribution, queries were performed across the following digital repositories of biological collections: the Global Biodiversity Information Facility (GBIF) and Global Ant Biodiversity Informatics (GABI). GBIF query records found under https://doi.org/10.15468/dl.wvqpbn and https://doi.org/10.15468/dl.mcg2u9, the latter of which supplemented the query on insects by specifically targeting vespid wasps. We applied the following filters to our queries:

1. Records confined to the global tropics (which was important for defining tropics-wide endemism later on, see **1.4**)
2. Specimen-based data (i.e., excluding observational data to minimize species/taxonomic uncertainty)
3. The following taxonomic categories:
    a. Vertebrate taxa: Birds (Aves), mammals (Mammalia), amphibians (Amphibia), and reptiles (Reptilia)
    b. Invertebrate taxa: Soil-dwelling annelids, apids (Apoidea), arachnids (Araneae), blattodeans and isopterans (Blattodea/Isoptera), dipterans (Diptera), odonates (Odonata), terrestrial gastropods (Gastropoda), hemipterans (Hemiptera), lepidopterans (Lepidoptera), orthopterans (Orthoptera), trichopterans (Trichoptera), and vespid wasps (Vespidae)
    c. Angiosperm families: Asteraceae, Fabaceae, Orchidaceae, Poaceae, and Rubiaceae
    d. Pteridophyte lineages: All fern taxa (Polypodiopsida)

This resulted in over 23 million records, of which we excluded records situated in marine environments or with spatial inconsistencies, and which we verified against locality descriptions in the database. For records lacking geographic coordinates or with misaligned coordinates, we manually georeferenced the entries by cross-referencing the locality descriptions provided in the original metadata with the general occurrence data available in the GBIF database (https://www.gbif.org/). When locality descriptions could not be matched using GBIF, we used OpenStreetMap (https://www.openstreetmap.org) to identify and assign approximate coordinates based on place names (e.g., municipalities, natural landmarks) mentioned in the records. No coordinates were inferred based on species distribution alone; only explicit locality information from the original data was used. Taxonomic accuracy was ensured via validation against the Catalogue of Life Checklist 2023 (https://www.catalogueoflife.org/), with synanthropic species excluded. When a species had undergone multiple name changes over time, we tracked its synonyms and systematically replaced the original name with the latest accepted/valid name (i.e., the updated taxonomic name). In addition, names classified as nomina dubia (of uncertain identity or taxonomic validity) were removed, and the corresponding records were excluded from the analyses. Post-processing, including coordinate validation and taxonomic checks using the BioDinamica[4] GBIF data-cleaning module, yielded a final dataset of 8,619,185 records of 300,228 species across the tropics.

1.2 Accounting for sampling bias in biodiversity data

Sampling bias, i.e., the bias resulting from the geographic and taxonomic gaps in biodiversity data, is a common issue when dealing with biodiversity data and subsequent modeling[5–8]. Here, we account for this bias by implementing a previously developed method - the Uniform Sampling from Sampling Effort (USSE) framework[3]. USSE works by incorporating sampling effort into the biodiversity prediction models. We proxy sampling effort by estimating a uniform and maximum sampling density using a kernel function with a 50 km radius. The prediction models are trained with the available biodiversity data, and these data are subsequently replaced with the maximum, uniform sampling effort we estimated. Thus, we could predict biodiversity patterns based on environmental variables, yet also accounting for sampling effort and significantly minimizing the effects of these gaps in the spatial modeling of these metrics (as demonstrated in previous studies)[3].

1.3 Calculating richness and endemism

Having sourced the data, and applied USSE, we calculated species richness and endemism using equal-area hexagons (approximately 42 km²) as sampling units in order to use these as dependent variables in the biodiversity modeling (**1.4**). We defined these as:

1. Species Richness: Total species count per hexagon.
2. Endemism: Geographic restriction of species per hexagon, quantified via the Corrected Weighted Endemism Index (WEIc)[9]. The value of a species is inversely proportional to its total range across global tropics (ranging from 0-1). Higher weights are assigned to species with smaller range sizes, meaning values closer to 1 represent more endemic species. This value is summed across all species in a cell.

1.4 Compilation of environmental variables for biodiversity modeling

We compiled climatic and topographic variables, and additionally modeled vegetation structure through a variety of environmental inputs (see below). All environmental predictors were based on their native 1 km² spatial resolution which for model training were aggregated to a mean per-hexagon (as defined in **1.3**).To address potential multicollinearity and model overfitting from the high variable count, we minimized dimensionality through principal component analysis (PCA)[10] using correlation-based covariance matrices. This approach synthesizes variables into orthogonal axes (linear combinations of original variables) that capture environmental gradients across grid cells. The PCA generated composite raster layers[4] representing synthesized variables, enabling interpretation of multivariate environmental patterns without individual variable scrutiny. For climate predictors, we retained the top four PCA axes (selected via Kaiser's eigenvalue criterion[11], explaining 89.02% of cumulative variance in WorldClim-derived variables (Extended Data Tab. 1). PCA rasterization was executed using BioDinamica [4].

Climate

To characterize climate, we used data from WorldClim[12], which includes temperature and the following precipitation variables:

1. Annual Mean Temperature.
2. Mean Diurnal Range (mean monthly difference between maximum and minimum temperature).
3. Isothermality (Mean Diurnal Range / Annual Temperature Range) (×100).
4. Temperature Seasonality (standard deviation ×100).
5. Maximum Temperature of the Warmest Month.
6. Minimum Temperature of the Coldest Month.
7. Annual Temperature Range (Maximum Temperature of the Warmest Month - Minimum Temperature of the Coldest Month).
8. Mean Temperature of the Wettest Quarter.
9. Mean Temperature of the Driest Quarter.
10. Mean Temperature of the Warmest Quarter.
11. Mean Temperature of the Coldest Quarter.
12. Annual Precipitation.
13. Precipitation of the Wettest Month.
14. Precipitation of the Driest Month.
15. Precipitation Seasonality (Coefficient of Variation).
16. Precipitation of the Wettest Quarter.
17. Precipitation of the Driest Quarter.
18. Precipitation of the Warmest Quarter.
19. Precipitation of the Coldest Quarter.

Topography

We used two topographic variables at a spatial resolution of 1 km²: 1) Elevation [13], and derived from it using its original spatial resolution, 2) Slope.

Vegetation structure data

Vegetation structural attributes were characterized using Light Detection and Ranging (LIDAR) [14] and Moderate-Resolution Imaging Spectroradiometer (MODIS) datasets. Canopy height (2020), derived from machine learning-interpolated LIDAR data,[14] served as a direct metric for differentiating vegetation structures and distinguishing natural versus anthropogenic habitats. Additionally, the Normalized Difference Vegetation Index (NDVI) was calculated from NASA's MYD09A1 [15] product (2020; 1 km² resolution) to assess vegetation stress, density gradients, and seasonal dynamics. Monthly NDVI variance per grid cell was aggregated annually to capture seasonality patterns and land-use contrasts. To mitigate multicollinearity and overparameterization risks, principal component analysis (PCA) was applied to these variables of NDVI mean and variance and canopy height (**Tab. S1**). The first PCA axis (again, selected via Kaiser's eigenvalue criterion) explained 71% of environmental variation and was retained for subsequent modeling (**Tab. S1**, PCA axis 1).

Table S1. Proportion of explanation of each PCA axis of the variables of vegetation structure.

PCA components	PCA axis 1	PCA axis 2	PCA axis 3
Standard deviation	1.46	0.80	0.50
Proportion of Variance	0.71	0.21	0.08
Cumulative Proportion	0.71	0.92	1.00

1.5 Algorithm Evaluation for Spatial Predictions of biodiversity metrics

Having gathered and compiled biodiversity data (**1.1**), accounted for sampling bias (**1.2**), and compiled the required environmental variables (**1.3**), we were able to directly model species richness and endemism in 2020 on a pixel-by-pixel basis . To this end, we evaluated a range of modeling approaches in order to select the algorithm with the highest possible predictive performance: Deep Neural Network (DNN)[16], Generalized Linear Model (GLM)[17], Generalized Additive Model (GAM)[18], LASSO[19], MARS[20], Random Forest (RF)[21], and Support Vector Machines (SVM)[22].We selected deep learning models, specifically DNNs, as these are particularly well-suited for capturing complex patterns in data, and indeed, they outperformed other models in our tests (see **Tab. S2**). Model configurations were as follows:

- GLM: Used a Gaussian distribution, appropriate for modeling continuous biodiversity indices expected to approximate a normal distribution.
- GAM: Applied spline functions to each predictor to account for nonlinear relationships, also assuming a Gaussian error structure.
- LASSO: Applied cross-validation to determine the optimal regularization parameter (λ), improving generalization by penalizing overly complex models.
- MARS: Allowed up to 100 models with a maximum interaction degree of 3, capped at 50 nodes, and included a penalty of 2 to control overfitting.
- RF: Built using 300 decision trees, aggregating results to improve robustness and reduce variance.
- SVM: Configured for epsilon-regression, enabling the model to predict continuous outcomes within a margin of error.

The DNN used for regression consisted of five hidden layers with 64 neurons each. Kernel regularization ($\lambda = 0.01$) was applied to layers 1 and 3 to discourage overly large weights, and dropout layers (20%) were used after those layers to reduce overfitting. A final hidden layer with 64 neurons fed into a single-neuron output layer. The model was trained via backpropagation to minimize prediction error, and 20% of the dataset was held out as a validation set to monitor performance during training. We experimented with several DNN architectures to identify the most effective configuration. These included variations in the number of neurons, the use of regularization and dropout, and the number of layers:

1. 32 neurons → dropout → 64 neurons → single neuron.
2. 64 neurons → dropout → 64 neurons → single neuron.
3. Dual 64-neuron layers (regularization + dropout) → single neuron.
4. Five 64-neuron layers (layers 1/3 regularized) → 64 neurons → single neuron.
5. 128 neurons (regularized) → 128 neurons (dropout) → 64 neurons (regularized/dropout) → 32 neurons → single neuron.
6. 128 neurons (regularized) → 128 neurons (dropout) → five 64-neuron layers (layers 1/3 regularized) → 64 neurons → single neuron.

Cross-validation of models

We carried out the cross-validation of these models using the mean squared error (MSE) and randomly splitting the data into five sets (80% used for training and 20% for testing). As seen in **Table S2**, we selected the DNN because it had the lowest rate of error (2.79 MSE for richness, and 4.26 MSE for endemism), and the highest predictive performance (R^2 0.92).

Table S2. Cross-validation of different algorithms. Mean squared error (MSE) values for each algorithm and the R^2 of the relationship between observed and predicted values for the algorithm with the lowest MSE (DNN), considering the relationship with sampling effort.

Algorithm	MSE Species richness	MSE Endemicity
DNN	2.79	4.26
GAM	30.48	43.88
MARS	9.87	15.69
RF	3.99	4.34
GLM	5.81	5.73
LASSO	16.00	20.80
SVM	11.08	14.79
DNN R^2	0.92	0.89

Modeled biodiversity metrics

Once we finished modeling, we first adjusted the per-pixel output values from hexagon-based predictions to 1 km² by dividing by a factor of 0.023. While this assumes a linear scaling of biodiversity with area, all pixels were equally affected by this adjustment, making comparisons across pixels consistent. Hence, we defined species richness and endemism (WEIc) following **1.3**, but at the scale of 1 km². Note, endemism is thus based on species' tropical ranges.

Finally, we cropped our modeled results to the area of Brazil, which resulted in a final dataset of 843,574 unique records and 34,333 species.

1.6 Creating the baseline biodiversity scenario

To be able to compare current biodiversity patterns with a hypothetical scenario under full potential restoration of biodiversity, we needed to establish a “baseline” of this potential biodiversity – without human-driven LU. To this end, we first created a model of vegetation structure, which incorporated variables linked to vegetation dynamics [23–27] . With the vegetation structure index as a dependent variable, we trained and validated this vegetation structure model. We used the following variables as predictors:

- **Land Use in 2020**: Global 2000–2020 Land Cover and Land Use Change maps [28].
- **Elevation & Slope:** Global Multi-Resolution Terrain Elevation Data 2010[13]
- **Climate**: Represented by the first four PCA axes, capturing 89.02% of climatic variation.
- **Soil**: Derived from SoilGrids[29] (0–5 cm depth), including 11 variables: bulk density, cation exchange capacity, coarse fragments, clay fraction, total nitrogen, organic carbon density/stock, pH, sand/silt fractions, and soil organic carbon (all at 1 km² resolution). To mitigate multicollinearity, soil variables underwent PCA, retaining the first two axes (Kaiser’s criterion), which explained 68.25% of cumulative variance

Following the same cross-validation process that we used for the biodiversity models described above (**1.5**), we assessed predictive performance (80% training, 20% testing) using Mean Squared Error (MSE). MSE was prioritized over AUC/TSS due to the continuous nature of biodiversity indices, which require accuracy in magnitude and spatial variation. The Deep Neural Network (DNN) with architecture 5 achieved the lowest MSE (0.228) and highest correlation (R^2=0.8274), outperforming other algorithms (GAM (0.266), MARS (0.281), RF (0.369), GLM (0.522), LASSO (0.526), and SVM (0.537)).

Having selected the best-performing algorithm, we then used this vegetation model in the original biodiversity models explained in **1.5** to predict the biodiversity baseline. Specifically, we replaced all anthropogenic LUs in 2020 (i.e., croplands, urban areas, roads, and pastures) with the modeled vegetation expected for the biomes expected in those areas[30] (e.g., tropical savannas and grasslands, tropical dry forests, moist broadleaf forests, etc.). "Potentially restored" vegetation is used as the input for the biodiversity models to estimate baseline biodiversity. All other remaining variables were kept constant. For baseline endemism, species’ range sizes were based on current distributions, but the index values reflected the predicted pristine environmental conditions. Naturally, we were not able to validate this resulting hypothetical scenario with data (as this would require observations of these areas without anthropogenic influence), yet, by approximating “pristine” habitat and vegetation patterns we are able to compare current and “baseline” biodiversity patterns.

Nonetheless, we fully recognize that in this comparison we assume the full restoration of biodiversity in currently human-influenced areas of Brazil (as illustrated in **Fig. 4C**, and **S4**), which may not always be possible or desirable to those living in these areas (albeit legally required). Such landholders/owners may include large landholders, indigenous, traditional, and local communities, and restoration action should involve the participation and agency of these peoples. However, in illustrating the areas with highest potential restoration and highest deficit in FC compliance, we have focused specifically on the role of large landholders/owners. Albeit full restoration might not be attainable for all landholders/owners (as illustrated in **Fig. 4C, S4**), we are able to indicate areas where increased, due compliance with existing policy infrastructures could yet lead to substantial gains in biodiversity.

2. Land tenure data compilation

Building on Pacheco & Meyer (2022), we identified and compiled the following land tenure categories and sources in Brazil:

1. Private lands & claims (*imóveis rurais*): We defined the rural properties registered on the CAR as "private lands & claims", as many of these registrations may not necessarily reflect legal titles – although the majority do reflect legitimate land claims (Freitas et al., 2017; Sparovek et al., 2019). Sourced from Imaflora (de Freitas et al., 2018).
2. Rural settlements (*assentamentos rurais*): publicly-owned rural farmlands held by individuals or groups of families as a result of land reform. Sourced from Imaflora (de Freitas et al., 2018).
3. Protected areas (PAs) following definitions from the Ministry of Environment (Ministerio do Meio Ambiente, 2023):
    a. PA strict protection (*unidades de conservação de proteção integral)*: PAs under strict protection
    b. PA sustainable use (*unidades de conservação de uso sustentável*): PAs under sustainable use management
4. Indigenous lands (FUNAI, 2023),
5. Undesignated public lands: public lands under no formal designation or management (SFB, 2021)
6. Quilombola lands: lands belonging to communities of escaped enslaved people and their descendants (INCRA, 2023).

We also initially included private protected areas in our initial compilation (*reservas particulares do patrimonio natural*), sourced from ICMBio (the Chico Mendes Institute for Biodiversity Conservation), however, we excluded these from subsequent analyses as they covered an extremely small area (**Tab. S3, Fig. S1**).

Table S3. Land tenure data compilation. Total area is rounded to the nearest 100th km^2, and mean/min/max exclude properties <$1km^2$ as these were not relevant to subsequent analyses (in order to overlay data with biodiversity indicators).

Category	**Total area (km^2)**	**Mean parcel area (km^2)** (min/max)	**Source**
Private lands & claims	4,836,400	5 (1 - 26,896)	Imaflora
Rural settlements	307,800	37.3 (1 - 8,642)	
Undesignated lands	670,000	426 (1 - 15,955)	SFB
PA strict protection	487,000	802 (1 - 41,871)	MMA
PA sustainable use	574,200	2,107 (1 - 36,045)	
Private protected areas	4,500	14 (1 - 483)	ICMBio
Indigenous lands	1,023,500	2,197 (1 - 85, 297)	FUNAI
Quilombola lands	29,800	84 (1 - 7,198)	INCRA

In the process of compiling, cleaning, and preprocessing these data for further analysis, we identified self-overlaps (overlaps of indigenous lands on indigenous lands), as well as overlaps across categories (e.g., overlaps of private lands & claims in undesignated lands). As mentioned in the main text, rather than resolving these overlaps by arbitrarily imposing a hierarchy that prioritized certain categories over others, we opted for documenting these overlaps (**Fig. S1**), and reporting biodiversity analyses for each individual category (main text).

Nonetheless, we identified that the largest overlap of areas in Brazil was across undesignated lands and private lands/ & claims (*imóveis rurais*), with approximately 362,000 km^2 of overlapping areas (**Fig. S1**). The second largest overlaps were of private lands & claims in both categories of PAs (approximately 124,000 km^2 in strict protection PAs, and 112,000 km^2 in sustainable use PAs) (**Fig. 1**). While these figures already account for a pre-cleaning process of private lands & claims, which could indicate these are conservative estimates of overlapping areas, there are notwithstanding spatial errors that remain in these data. Additionally, considering that many properties are based on self-reported registrations as a part of the rural environmental cadaster (CAR), it is hence not possible to determine whether these overlaps represent actual conflicting land claims. Nonetheless, it is clear that regularizing these multiple and overlapping land claims remains an important governance issue. Other overlaps include those between indigenous areas and PAs (37, 131 km^2 in strict protection PAs, and 9, 616 km^2 in sustainable use areas). These overlaps are much smaller than the overlaps with private lands, but may also be due to particular usufruct clauses for indigenous peoples or local communities in some protected areas.

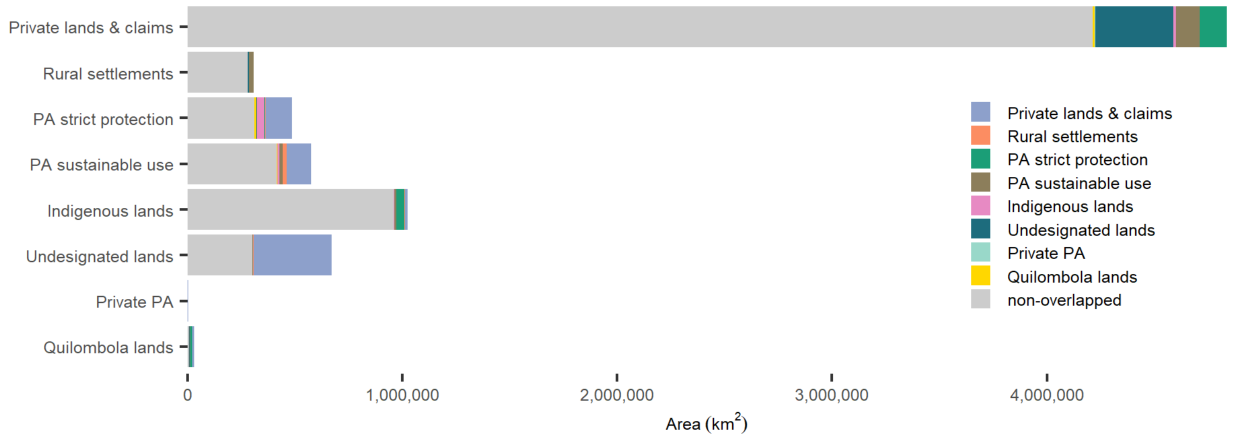

Figure S1. Distribution of land tenure in Brazil, per category (km^2), with overlaps across other categories highlighted in their respective color scheme (with overlaps mirrored across categories, e.g., over 300,000 km^2 private lands overlap with undesignated lands and vice versa). Note, while the overlaps of private lands and undesignated lands, as well as private lands and protected areas are most prominent, other categories also have substantial proportions of their lands overlapping with other categories. For instance, approximately 75% of quilombola lands overlap with other categories (mainly, PAs under strict protection and private lands & claims).

3. Disaggregation across biomes

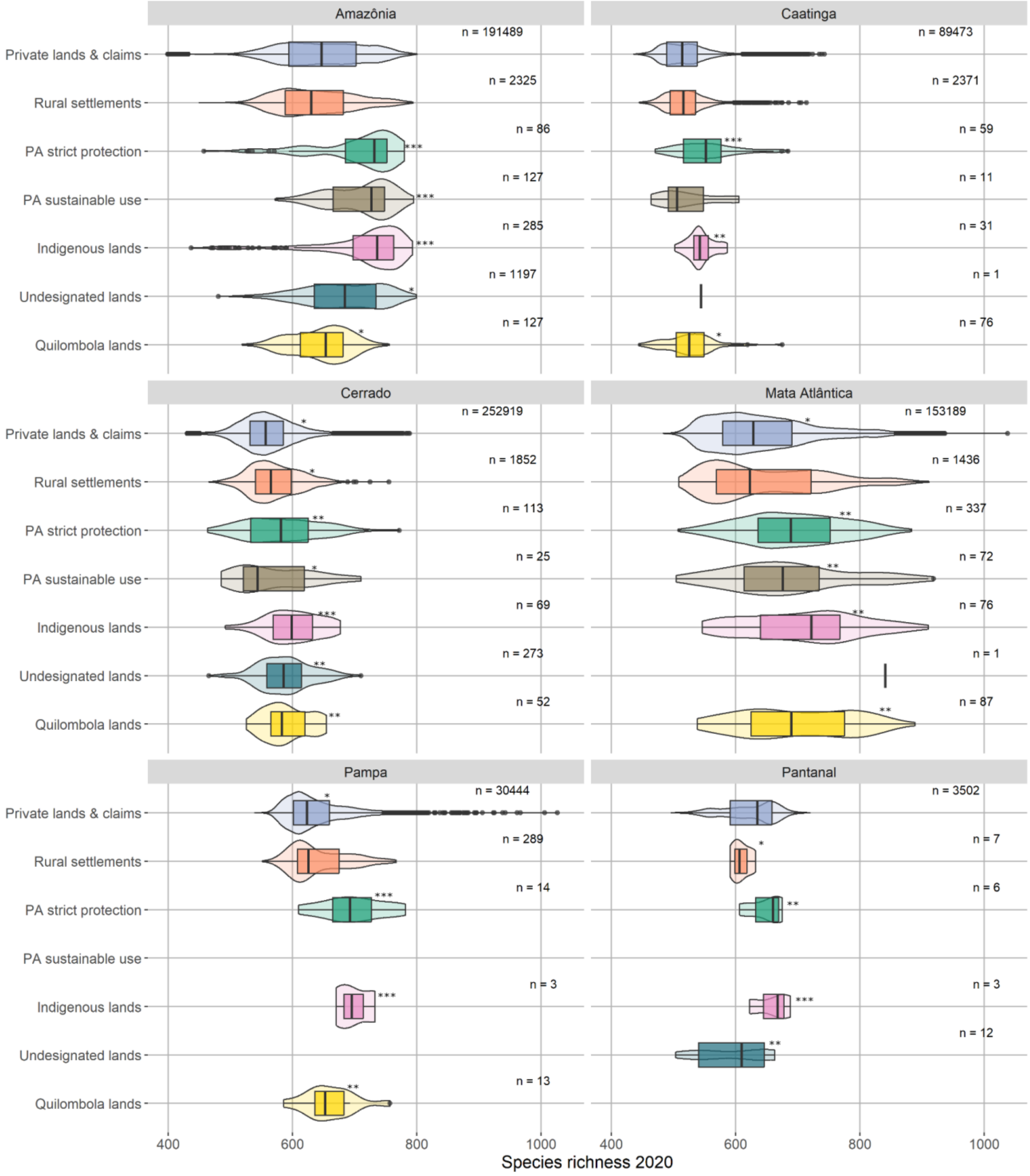

Figure S2. Boxplots of species richness in 2020 across tenure categories (with underlying distributions shown behind as violin plots) and disaggregated across biomes. The *n* of each data subset is labelled to the right of each category (note, this *n* is the resulting dataset post-processing as we exclude properties <1 km^2 and does not indicate the total number of properties/units within each category). We indicate Cohen's *d* values with asterisks to show standardized differences between tenure categories, i.e., the biodiversity in one category as compared against all others (values <0.2 indicate "negligible" differences and are shown with no *, <0.5 are "small" differences (*), <0.8 "medium" differences (**), and >0.8 are "large" differences (***) (confidence level 0.99).

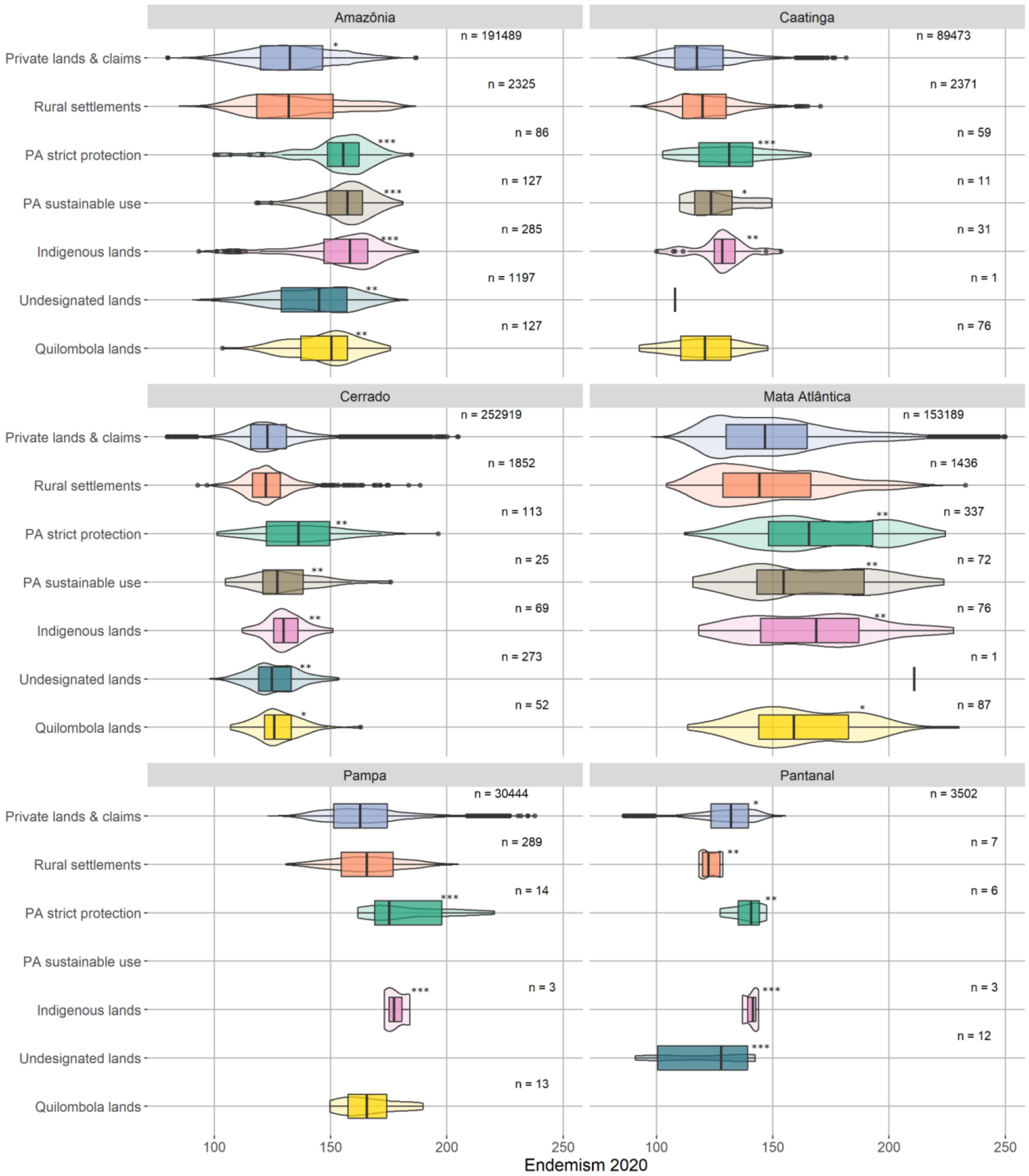

Figure S3. Boxplots of endemism index values in 2020 across tenure categories (with underlying distributions shown behind as violin plots) and disaggregated across biomes. The *n* of each data subset is labelled to the right of each category (note, this *n* is the resulting dataset post-processing as we exclude properties <1 km^2 and does not indicate the total number of properties/units within each category). We indicate Cohen's d values with asterisks to show standardized differences between tenure categories, i.e., the biodiversity in one category as compared against all others (values <0.2 indicate "negligible" differences and are shown with no *, <0.5 are "small" differences (*), <0.8 "medium" differences (**), and >0.8 are "large" differences (***) (confidence level 0.99).

Table S4. Cohen's *d* for results disaggregated across biomes (as seen in **S2-S3**). Values <0.2 indicate "negligible" differences, <0.5 are "small" differences, <0.8 "medium" differences, and >0.8 are "large" differences (confidence level 0.99), which are displayed in the "magnitude" column.

Tenure category	**Biome**	**Cohen's *d* richness**	**Magnitude richness**	**Cohen's *d* endemism**	**Magnitude endemism**
Rural settlements	Amazonia	-0.17491	negligible	0.084507	negligible
Indigenous lands	Amazonia	0.984209	large	1.148246	large
Private lands & claims	Amazonia	-0.15676	negligible	-0.36355	small
Quilombola lands	Amazonia	-0.03087	negligible	0.759019	medium
PA sustainable use	Amazonia	0.900606	large	1.214051	large
PA strict protection	Amazonia	0.821161	large	1.05533	large
Undesignated lands	Amazonia	0.485456	small	0.515015	medium
Rural settlements	Caatinga	0.043773	negligible	0.161736	negligible
Indigenous lands	Caatinga	0.731966	medium	0.629526	medium
Private lands & claims	Caatinga	-0.08424	negligible	-0.18377	negligible
Quilombola lands	Caatinga	0.278736	small	0.091899	negligible
PA sustainable use	Caatinga	0.169639	negligible	0.485805	small
PA strict protection	Caatinga	1.037905	large	0.86018	large
Undesignated lands	Caatinga	NA	NA	NA	NA
Rural settlements	Cerrado	0.252482	small	-0.07882	negligible
Indigenous lands	Cerrado	0.980164	large	0.517892	medium
Private lands & claims	Cerrado	-0.34931	small	-0.03161	negligible
Quilombola lands	Cerrado	0.730392	medium	0.273532	small
PA sustainable use	Cerrado	0.268284	small	0.527266	medium
PA strict protection	Cerrado	0.563954	medium	0.986132	large
Undesignated lands	Cerrado	0.676524	medium	0.165354	negligible
Rural settlements	Mata Atlantica	0.057767	negligible	-0.04625	negligible
Indigenous lands	Mata Atlantica	0.796558	medium	0.676199	medium
Private lands & claims	Mata Atlantica	-0.21994	small	-0.16153	negligible
Quilombola lands	Mata Atlantica	0.654501	medium	0.475379	small
PA strict protection	Mata Atlantica	0.598172	medium	0.764637	medium
PA sustainable use	Mata Atlantica	0.51271	medium	0.552058	medium
Undesignated lands	Mata Atlantica	NA	NA	NA	NA
Rural settlements	Pampa	0.143275	negligible	0.096398	negligible
Indigenous lands	Pampa	1.386279	large	0.836399	large
Private lands & claims	Pampa	-0.22562	small	-0.15093	negligible
Quilombola lands	Pampa	0.54293	medium	0.142614	negligible
PA strict protection	Pampa	1.356964	large	1.121048	large
Rural settlements	Pantanal	-0.33185	small	-0.59031	medium
Indigenous lands	Pantanal	0.812166	large	0.869577	large
Private lands & claims	Pantanal	0.146427	negligible	0.248608	small
PA strict protection	Pantanal	0.586409	medium	0.737684	medium
Undesignated lands	Pantanal	-0.64382	medium	-0.82071	large

4. Properties with potential overlaps

We repeated the assessment shown in Fig. 1 of the main text to assess whether these results were sensitive to excluding private lands and rural settlements with potential overlaps. While results were not qualitatively sensitive, Cohen’s *d* values did indeed change slightly, and are shown below in **Tab. S2**.

Note, this assessment did not include all the overlaps seen in **Fig. S1**, because it filtered for properties <1 km^2. We also focused on the overlaps between private lands/rural settlements and other categories (rather than the overlaps between PAs and indigenous lands) as these were a more concerning governance challenge with potential consequences for deforestation and biodiversity conservation.

Table S5. Summary of Cohen’s *d* with and without overlapping areas

Tenure category	**Including properties with potential overlapping areas**				**Excluding properties with potential overlapping areas**			
	Cohen’s *d* richness	**Magnitude richness**	**Cohen’s *d* endemism**	**Magnitude endemism**	**Cohen’s *d* richness**	**Magnitude richness**	**Cohen’s *d* endemism**	**Magnitude endemism**
Private lands & claims	-0.14269	negligible	-0.12421	negligible	-0.21589	small	-0.15457	negligible
Rural settlements	-0.12714	negligible	-0.06633	negligible	-0.05913	negligible	-0.03358	negligible
PA strict protection	0.783271	medium	1.107049	large	0.885911	large	1.145772	large
PA sustainable use	1.116381	large	0.989028	large	1.132433	large	1.00517	large
Indigenous lands	1.106467	large	0.83544	large	1.221667	large	0.872649	large
Undesignated lands	0.825147	large	0.299595	small	0.929747	large	0.334032	small
Quilombola lands	0.3396	small	0.451625	small	0.424928	small	0.48677	small

5. Species richness maps for vegetation surplus and deficit

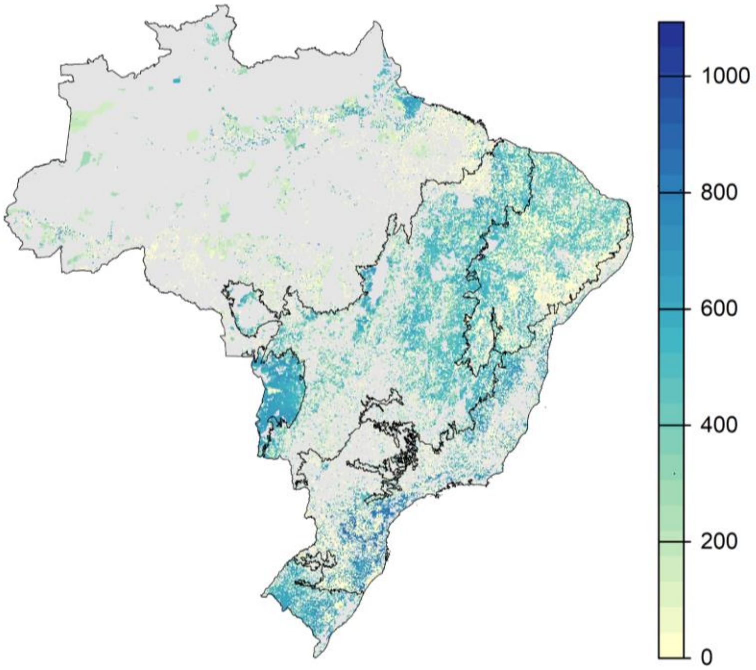

Figure S4. Current mean species richness (2020) in private lands & claims as well as rural settlements, weighted by the percent surplus in vegetation in compliance with the Forest Code.

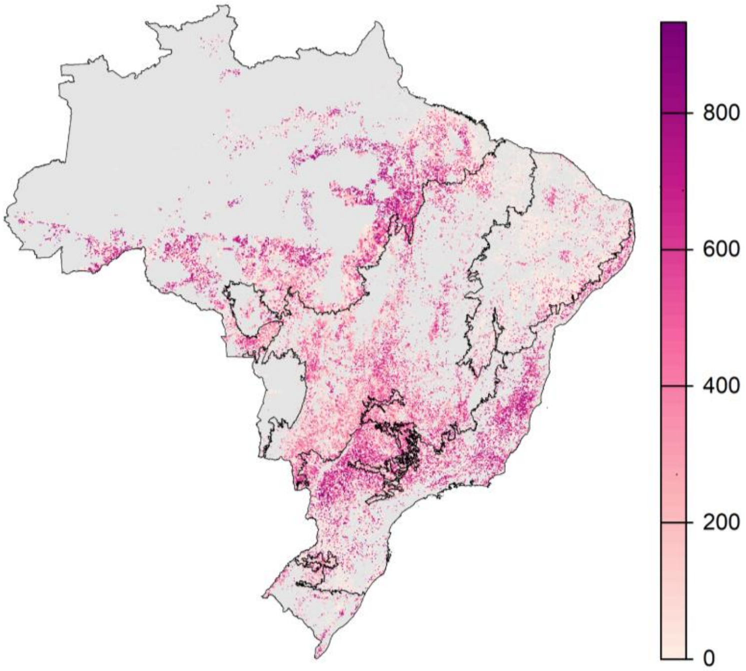

Figure S5. Species richness restoration potential in private lands & claims as well as rural settlements, weighted by the percent deficit in vegetation for compliance with the Forest Code (i.e., potential species numbers through full restoration and full compliance with the FC).

6. Supplementary discussion of limitations

Our analyses are subject to several limitations related to data availability, modeling choices, and spatial scale.

First, in downscaling biodiversity estimates from hexagonal units to pixels, we assumed linear scaling of biodiversity with area. We acknowledge that species-area relationships are not necessarily linear, however, this downscaling allows us to obtain a conservative estimate of richness and endemism per 1 km^2 pixel while keeping the proportional relationships among locations unchanged. The USSE approach showed high predictive capacity in proportional terms, meaning it captured the relative spatial relationship among localities and remained consistent with the estimated values at the hexagon scale. Because our metrics were originally estimated in large 42 km^2 hexagons, it is expected that these units encompass more species than a much smaller area such as a 1 km^2 pixel. The linear rescaling adjusts the magnitude expected at the pixel scale without altering the relative spatial gradients predicted by the model.

Second, we relied on a direct modeling approach that, while suitable for identifying broad biodiversity patterns across large spatial extents, does not allow inference about species-specific distributions. Incorporating species-level occurrence data, alongside improved temporal monitoring, would enable comparisons of community composition across tenure categories and represents an important research frontier. Third, because our data compilation focused on species' tropical ranges, our estimates may overemphasize globally distributed species while underrepresenting species confined to the tropics. Fourth, our broad spatial-scale analysis across Brazil facilitates the identification of general patterns but necessarily abstracts from local contexts. This is most relevant for private lands, where biodiversity varied most across properties.

Finally, biodiversity patterns are neither spatially nor temporally independent; species occurring in one tenure category are likely to influence biodiversity in adjacent categories. While resolving conflicting land claims remains pressing, explicitly accounting for such spatial interdependencies could further improve conservation prioritization strategies.

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