The multitaxa functional diversity increases the resilience of biological natural capital in the Amazon

Abstract

1. The resilience of biological natural capital in the Amazon is strongly influenced by the functional diversity of multitaxa, which promotes the stability and sustainability of the ecosystem. However, biological natural capital, driven by multiple dimensions of biodiversity, is often underestimated by focusing on taxonomic dimension, such as richness and abundance.

2. We applied a multitaxa and trait-based approach to assess how functional diversity supports natural capital. Using a dataset including woody plants, bees, frugivorous butterflies and songbirds, we created two indices: Biological Natural Capital Resilience (BNCR), the proportion of biological assets needed to maintain natural capital integrity, and Biological Natural Capital Uniqueness (BNCU), the proportion of natural capital sustained by species' functional uniqueness.

3. BNCR results show that in general more than 80% of biological assets to maintain the integrity of natural capital, and that the BNCR index reached the highest value when all taxonomical groups are combined. These results reveal that natural capital strongly depends on biological assets and underscore the importance of multi-taxa approaches for assessing ecosystem resilience.

4. BNCU values show that a substantial portion of natural capital integrity (from 46.22% to 64.23%) depends on a small subset of functionally unique species, indicating that the loss of few species, which play irreplaceable ecological roles, rapidly reduces ecosystem functioning.

5. Synthesis and applications: This study presents a trait-based framework integrating functional diversity into biological natural capital accounting, capturing both ecosystem resilience and species uniqueness across multiple taxa. It provides ecologically grounded,

standardized, and reproducible indicators that move beyond single-taxon or purely taxonomic approaches. By embedding these indicators into natural capital accounts, the framework supports conservation prioritization, restoration planning, impact assessment, trend monitoring, and scenario testing, offering a practical methodology to evaluate and manage the multiple dimensions of biodiversity within natural capital assessments.

Keywords: *Biological Assets; bees; butterflies; birds; flora; Functional Diversity; National Forest of Carajás*

Introduction

The concept of natural capital recognizes the value of natural resources in relation to a product or service, and was explicitly developed in the 1970s and popularized in the 1990s (Gómez-Baggethun & Groot 2010, Ovando 2021). In economics, "capital" refers to the stock of materials or information that generate a flow of services that provide benefits to people (Costanza et al. 1997). Thus, natural capital expresses the stock of renewable and non-renewable natural resources that provide benefits to humanity through ecosystem services (Costanza & Daily 1992, MEA 2005). The natural capital account is a practical approach to environmental management that focuses specifically on understanding and documenting the state of nature and measuring and assigning value to ecosystem services (Oliver 2018, Ovando 2021). It contributes to setting environmental policy goals, because it identifies the status of an environmental asset and shows whether the current use of natural resources is sustainable over time (Bright et al. 2019). In addition, assessing the state of natural capital is a compelling tool for conservation, communication, and awareness of regional natural heritage (Oliver 2018). This approach also places natural heritage at the same level of other forms of capital (e.g., financial, industrial, social, and human) and underscores its importance to the economic sector (Oliver 2018). Natural capital has also become relevant to the private sector (Guerry et al. 2015), as an important tool for assessing natural resource business dependence, risk analysis, and supply chain management (Natural Capital Coalition 2016). Therefore, the concept of natural capital has emerged as a valuable framework for understanding and valuing the stock of renewable and non-renewable natural resources, and rises as instrumental to the management of natural resources. However, it is crucial to recognise the potential pitfalls associated with the concept of natural capital, primarily the reduction of nature to monetary values, which leads to the undervaluation of essential assets and the oversimplification of ecosystems (Mace, 2019).

The United Nations Statistics Division (UNSD) has been leading the development of the System of Environmental-Economic Accounting - Ecosystem Accounting (SEEA EA) framework, which aims to standardize the quantification of ecosystem asset stocks, such as biodiversity, and ecosystem service flows over time (UNCEEA, 2021). Biodiversity is an essential ecosystem asset of natural capital, since it encompasses all forms of diversity of living components of ecosystems, and its multidimensionality (e.g. taxonomic diversity, functional diversity, genetic diversity and diversity of interactions) makes it a key element at all levels of the ecosystem function hierarchy, both as a regulator of ecosystem services, as a final ecosystem service, or as a good of valuation (Mace et al. 2012). In SEEA EA, biodiversity is defined according to the Convention on Biological Diversity (Secretariat of the Convention on Biological Diversity 2020) as "biological diversity means the variability among living organisms from all sources," and its components are classified into three categories: ecosystem diversity, species diversity, and genetic diversity. In natural capital accounting biological natural capital specifically refers to the stock of biological components, or biological assets, such as species, traits, and ecological functions that contribute to ecosystem services (Mace 2019). Despite its importance for natural capital, current estimates of biological natural capital often focus on biomass or species richness and rarely incorporate other dimensions of biodiversity (Smith et al. 2017). Part of the difficulty in integrating these aspects, particularly dimensions beyond the taxonomic, comes from the fact that their values mainly reflect ecological significance rather than producing estimates directly actionable for management, leading to underestimation of ecosystem resilience and species’ contributions to ecosystem functioning (Mace 2019)). Moreover, while SEEA-EA recognizes the many aspects of biodiversity, its primary focus is on ecosystem diversity, giving broad principles for accounting for biodiversity rather than detailed guidance on what sorts of data should be utilized and evaluated (Bradon et al. 2021).

In order to increase the valuation of biodiversity in natural capital accounting, researchers have been advocating for approaches that integrate multiple elements of biodiversity, such as interaction diversity, functional diversity, and genetic diversity, as fundamental components of natural capital accounting (Coates et al. 2020). In this sense, Brand (2009) proposed that among the dimensions that should be considered in natural capital accounting are those related with the ecological resilience and the vulnerability of the natural capital assets. Functional traits and functional diversity are key to ecological resilience, with similarities among species creating functional redundancy that buffers ecosystems against disturbances, and unique traits indicating vulnerable functions. Together, redundancy and uniqueness offer valuable tools for assessing biodiversity, ecosystem integrity, and adaptive capacity, often overlooked in natural capital accounting (Ricotta et al., 2016; Díaz & Cabido, 2001; Brand et al., 2009; La Notte et al., 2017). Incorporating functional diversity into natural capital accounting potentially provides critical insights into ecosystem integrity, the capacity to resist and adapt to global changes, and the sustainable long-term use of natural resources, while improves the assessment of ecosystem contributions - enabling more accurate evaluations of the resilience and vulnerability of natural assets for conservation and management decisions.

Amazon forest is the world's largest tropical forest, housing more than a third of the world's biodiversity and providing essential ecosystem services to humanity at local, regional and global scales (Mittermier et al. 2003). Despite this importance, high deforestation and habitat degradation rates have been causing biodiversity loss in Amazon, affecting the forest resilience to human activities and climate change (Levine et al. 2016), compromising the forest's capacity to sequester carbon (Gatti et al. 2022) and changing its hydrological cycle, with potential negative consequences for the climate at global scale (Lovejoy & Nobre 2019). Amazon biodiversity contains a large diversity of unique traits in the community, as a consequence of the evolutionary strategy of strong differentiation between species (Kraft et al. 2008). Studies in tropical rainforest ecosystems, including the Amazon forest, have shown that rare and highly functionally unique species often contribute disproportionately to ecosystem functioning, meaning that the loss of a few functionally unique species can lead to a significant reduction in ecosystem stability and natural capital integrity (Leitão et al. 2016; Dee et al. 2019).

Given the high biodiversity and ecological complexity of the Amazon, this study uses a multi-taxa, trait-based approach to evaluate how functional diversity reflect the resilience and uniqueness of Amazonian natural capital under species loss scenarios. Specifically, we investigate the extent to which functional redundancy buffers ecosystem integrity and how functional uniqueness shapes the vulnerability of these communities. Therefore, we propose the following testable hypotheses: (1) the resilience of natural capital in Amazon is mainly sustained by biodiversity, meaning most of biological assets need to be maintained to conserve natural capital integrity; (2) due to the high uniqueness of these Amazon communities, a substantial portion of natural capital integrity relies on a relatively high number of unique species, making natural capital in Amazon particularly vulnerable to species loss.

Material and Methods

Study area

The study was carried out in the National Forest of Carajás, Eastern Amazon (Pará State). This forest is a sustainable use protected area covering more than 3,930 km^2 and its vegetation is characterized mainly by an Open Ombrophilous Forest, with local variations related to changes in soil and relief (Barbosa-Silva et al. 2022). In the steep areas, the "forest with lianas" predominates - characterized by a medium biomass with low density, with more light penetration in its interior. The region of the study area stands out for its significant natural capital in terms of biodiversity, carbon stock, water regulation, climate regulation and food security (Neugarten et al. 2015) . However, little is known regionally about its role in natural capital, highlighting both its great potential for climate regulation via evapotranspiration (Pontes et al. 2017) and the vulnerability of its biodiversity-driven ecosystem services under scenarios futures (Costa et al. 2018). Our study does not aim to comprehensively sample or quantify all biodiversity or natural capital of the whole Amazon. Instead, we focus on a representative local pristine dataset to explore fundamental mechanisms linking functional diversity to the stability of biological natural capital.

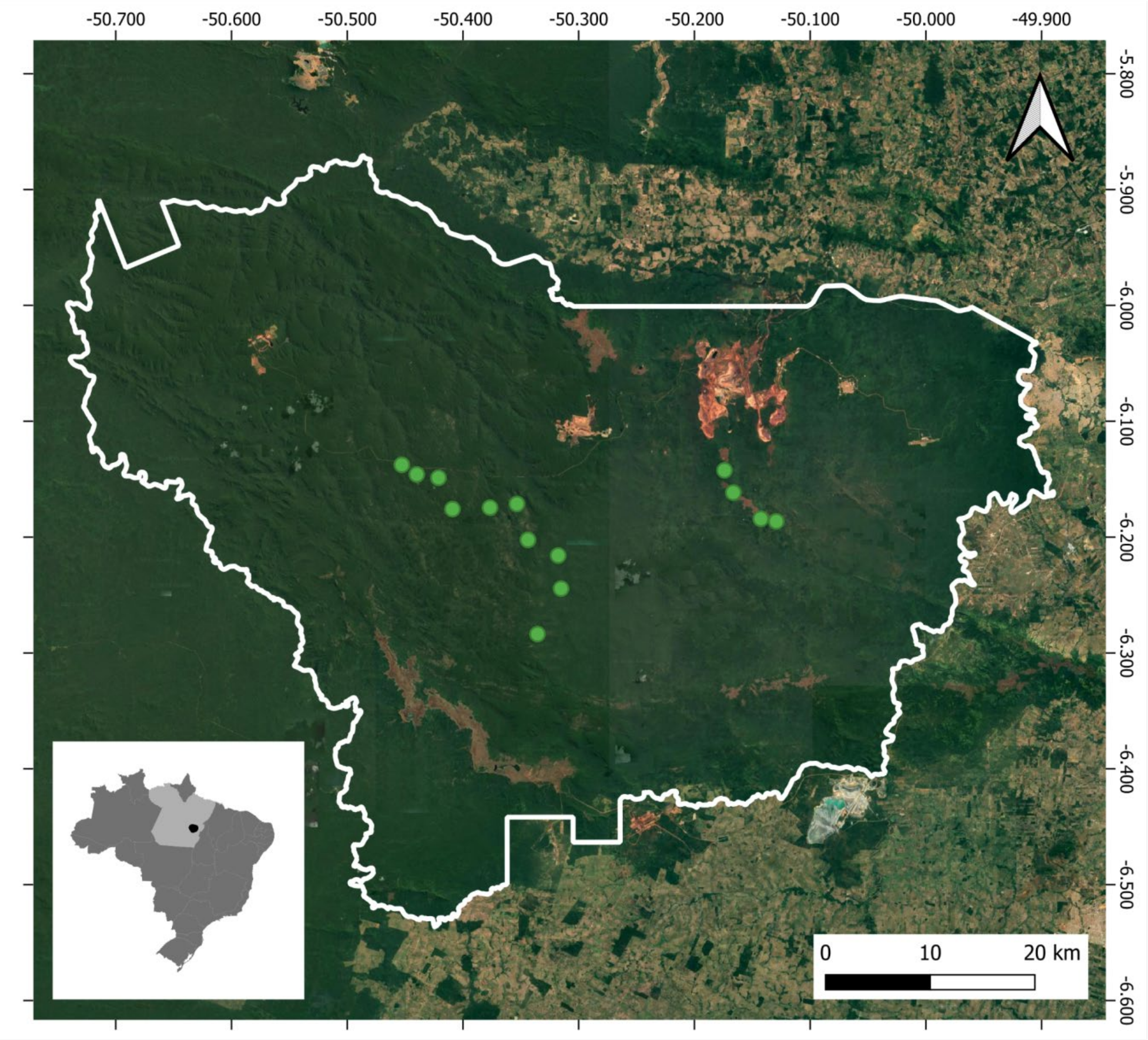


Figure 1. Study area and sampling locations. The white line delineates the boundaries of the Carajás National Forest, and the green dots represent the sampling points. The background image is a satellite view from Google Earth. The inset map (bottom left) shows the location of the study area within Brazil: the dark grey area represents Brazil, the light green indicates the state of Pará, and the black dot marks the location of the Carajás National Forest.

Biodiversity sampling

In order to evaluate the biodiversity assets in the natural capital account, we conducted a comprehensive survey of four groups of organisms across 14 pristine forest sites that were at least 1.5 km apart in November 2019 and March, April, May, August and September 2022. These dates were selected avoiding the coldest period of the year ,when biodiversity levels tend to be lower due to reduced biological activity, and respecting safety protocols due to the COVID pandemic during the research period. The selection of these groups was based on their significance in providing and sustaining ecosystem functions. Bird communities were examined by detecting their songs through the use of Audiomoth 1.0.0 digital audio recordings (Hill et al, 2019) at each of the 14 sampling sites. The devices were positioned in the undergrowth of the forest, approximately 1.5 m above ground level. For bird identification, we selected minutes between 5:00 and 9:00 and between 17:00 and 19:00 from the recordings, and vocalizations were identified by a specialist. Frugivorous butterflies (Nymphalidae) were sampled using Van Someren-Rydon model traps baited with a fermented mixture of banana and beer for 48 hours, at the same 14 sampling sites. We set up two traps by sampling site, positioned in both the understory (ca. 1.5m above ground) and near the canopy (ca. 20-30m above ground). Each trap was monitored every 48 hours and kept at each location for 6 days, following the methodology outlined by Uehara-Prado et al. (2005). After identification, the specimens were placed in the entomological collection of the Museu Paraense Emílio Goeldi (MPEG) and identified with the help of literature that included plates with color photographs, as well as "Butterflies of America" (Warren et al., 2016). To sample bees, we utilized three sampling methods: aromatic traps, honey traps and flower visitors. Aromatic traps were used to attract orchid bee males with four artificial essences (Eucalyptol, Vanillin, Eugenol and Methyl Salicylate). Honey traps were used to attract foraging bees from both the understory and the forest canopy. A honey and water mixture (1:1) was sprayed in the vegetation and all bees collected. To sample flower visitors we observed all open flowers and collected all visitors for two non-consecutive hours per sample in each site. Three samples were carried out in each site. Bees were identified by specialists and deposited in MPEG. Lastly, to sample woody plants, we conducted species surveys in 20 m x 100 m plots at six of the 14 sampled sites followed by random collections in the vicinity of the plots to supplement data on fruiting plants, which are essential for accurate identification by taxonomists. All plants have their diameter at height breast (DBH) and canopy height measured, and we kept the records of those with DBH > 10cm. Plant exsiccatae were also deposited at the.

For all taxonomic groups, we aggregated all spatial and temporal sampling data into a single pooled community, representing the total set of species detected across all sampling points and dates. While these communities do not aim to represent the full regional species pool of each taxonomic group, it represents from 71% to 93% of the estimated total species richness for the surveyed taxa (Supplementary Material I). This approach allows us to analyze overall functional patterns at the landscape scale, while acknowledging the limitations inherent to sampling effort, detectability, and seasonal variation.

Functional Diversity Indexes

We use functional diversity measures to infer the biological resilience and uniqueness of natural capital maintained by biological assets. These measures are based on the diversity of functional traits of communities, which in turn represent the diversity of ecosystem functions and services performed by communities in the ecosystem. For each taxonomic group sampled, we construct a database of functional traits, using both sampled species morphological measures and information from a free database. For bees, the selected traits were body mass, tongue length, distance between the inner margins of the eyes, spectrum of pollen hosts, level of sociality, and recognition of the species as a crop pollinator. For Lepidoptera, the selected traits were body size, proboscis length, forewing width, length from thorax to abdomen, presence of camouflage colours in the wings, presence of blemishes in the wings, iridescence in the wings or dorsal body parts, distance from the top to the bottom of the eye, and number of host plant species. For birds, the selected traits were body mass, Hand-Wing Index, habitat score, dietary composition, and foraging vertical distribution. For flora, the selected traits were type of dispersal and pollination syndromes, specific leaf area, wood density, and leaf phosphorus and nitrogen concentrations. Trait information for bees was gathered from open databases and literature, except for intertegular distance (used to estimate body size via allometric equations), which was measured by researchers. For birds and flora, all trait information was obtained from open databases, while for butterflies, all traits were measured directly by researchers, except for the number of host plant species, which was obtained from the literature (Supplementary Information II).

Species sampled whose functional traits were not measured or found in the database were excluded from the community for the calculation of functional diversity. For continuous functional traits, we used the mean value of the trait for each species, both in the case of measurements on the collected specimens and in the case of multiple measurements per species in the literature. From these trait databases, we calculate the Functional Richness (FRic), which represents the amount of functional trait space occupied by the community (Villéger et al. 2008). Species with available functional trait data represented 88.69%, 84.12%, 96.29%, and 91.29% of the total species richness of bee, bird, frugivorous butterfly, and tree communities, respectively. In terms of total abundance, these species accounted for 90.31% (bees), 80.40% (birds), and 98.86% (frugivorous butterflies). For trees, species with trait data contributed 65.81% of the total basal area, calculated based on the diameter at breast height (DBH) of each individual.

To calculate FRic, for each group we first normalized the continuous traits and log transformed them to avoid the influence of variables with high standard deviation and extreme values (Legendre & Legendre 2019). We then performed a Principal Coordinate Analysis (PCoA) with three dimensions (scores) for each taxonomic group to standardize the numbers dimensions among taxonomic groups. In all groups, we used the modified Gower distance (Pavoine et al. 2009), with equal weights for all traits, to calculate the PCoA, considering the different nature of the variables (continuous, proportional, or categorical). Categorical variables were transformed into binary variables using the package "ade4" (Dray & Dufour 2007) and proportional variables were considered as fuzzy variables. The PCoA procedure allowed us to integrate numerical and categorical variables and to reduce and standardize the number of dimensions between taxonomic groups. For all subsequent analyses, we use the three PCoA scores as functional traits, as proxies for the communities' functional space.

Biological resilience and uniqueness of natural capital

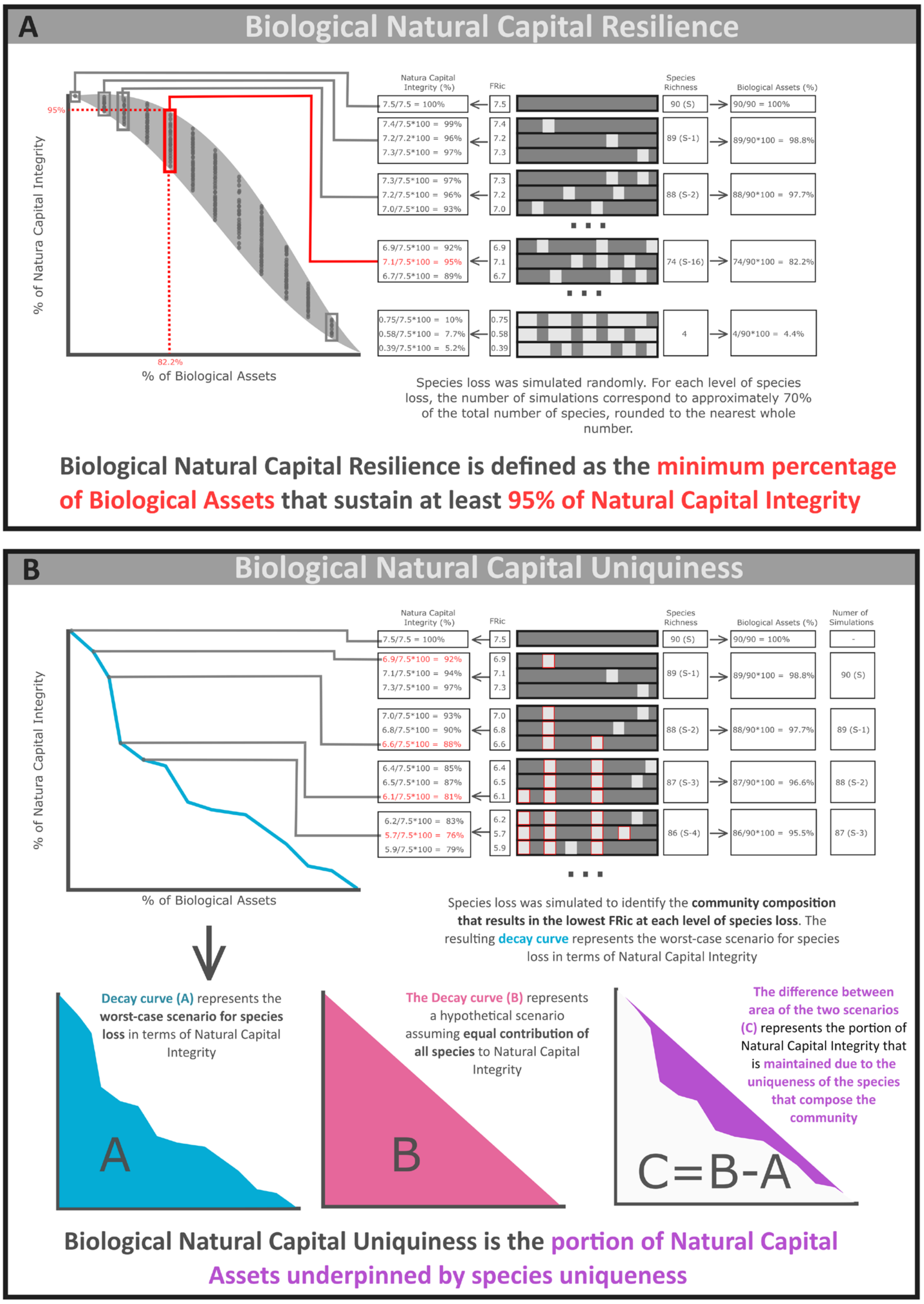
From the functional diversity indices calculated for the study sites, we derive the biological resilience and uniqueness of the natural capital through simulations of the loss of biological assets. Both resilience and uniqueness measures were based on the relation between biological assets and the integrity of natural capital sustained by biodiversity. For this we assumed the species richness as a proxy for the biological assets of natural capital, once it represents the biodiversity stock that sustains ecosystem functions and services, and is widely adopted in ecological assessments and policy frameworks (Coates et al. 2020). We also defined the integrity of natural capital as the capacity of biodiversity to support a broad range of ecosystem functions and services. To quantify this, we used Functional Richness (FRic) as a proxy of the integrity of natural capital, since it captures the extent of functional trait diversity within a community - higher FRic reflects a wider occupation of the functional niche space, indicating greater ecological role diversity and, consequently, a more functionally robust and resilient system (Villéger et al. 2008).

Through a random simulation of species loss, the resilience index proposed, named Biological natural capital Resilience (BNCR), depicts the percentage of total biological assets (species richness) that should be maintained to preserve the integrity of natural capital. This index was computed individually for each taxonomic group sampled, considering all species as the whole collection of biological assets. To do this, we consider that the values of FRic calculated for the whole community, representing 100% of the integrity of the natural capital supported by the biodiversity of each taxonomic group. We also consider, for each taxonomic group, the total number of species as 100% of the biological assets of natural capital.

To assess BNCR, for each taxonomical group, we simulated communities with random biological asset loss (species richness) and for each simulated community we calculated functional richness (FRic) standardized by the global FRic (FRic calculated with all species) for comparison (See Supplementary Information III, for simulation details). For each simulated community, the number of remaining species was converted to the percentage of total species and considered as the percentage of natural capital integrity. We then define Biological Natural Capital Resilience (BNCR) as the minimum percentage of biological assets that retains 95% of total FRic - which implies that a community that maintains 95% of its functional diversity is considered as intact as a community with 100% of its functional diversity (Figure 2A). While this 5% threshold is extensively supported by statistical literature (Cowles & Davis 1982, Murtaugh 2014) - based on frequentist statistics where a difference of less than 5% between populations of values represents a non-significant difference - it is possible to establish other values according to the objectives of natural capital accounting. This includes raising the threshold to higher values (more conservative goal) or lower values (more permissive goal).

In addition to BNCR for each taxonomic group, we also calculated the multitaxon BNCR by integrating all taxonomic groups and performing random simulation. For each taxonomic group both species richness and FRicwere expressed as a percentage of the group’s total values, thereby standardizing contributions from groups with different richness and functional scales For each level of species loss, we combined the previously within-group simulations across all taxonomic groups, using the percentage of remaining species as the proportion of biological assets and the corresponding sum of FRic as the percentage of natural capital integrity. The multitaxon BNCR was then defined as the minimum proportion of biological assets required across all groups to maintain at least 95% of total natural capital integrity, based on these standardized percentages. This approach preserves the relative contribution of each group to overall functional diversity while avoiding bias caused by differences in absolute FRic values.

To assess Biological Natural Capital Uniqueness (BNCU), we ran simulations of species loss again, this time not randomly, but assuming a worst-case scenario of natural capital integrity loss. Thus, for each level of biological assets loss (species loss), we calculated the FRic value for all possible communities and selected the one with the lowest FRic value. This value was standardized by global FRic of the taxonomic group and considered as the lowest percentage of natural capital integrity for that level of loss of biological assets. The species excluded at a given level of biological asset loss was also excluded at subsequent loss levels. Considering then the decay curve between the percentages of biological assets and natural capital integrity lost we then calculated the area under the curve (AUC) of the decay curve. This calculated area is then subtracted from the AUC of a hypothetical decay curve in which all species contribute equally to the integrity of natural capital, implying that the loss of a specific quantity of biological assets results in the same amount of natural capital integrity loss. We consider the difference between this and the AUC to represent the ratio of natural capital integrity supported by the uniqueness of species composing the natural capital assets. In terms of calculation, once both natural capital integrity and biological assets are represented as percentages, this hypothetical AUC corresponds to an isosceles right-angled triangle with an area of 0.5. Therefore, NBCU was calculated as 0.5 minus the AUC of the worst-case scenario, then multiplied by 2 to standardize the values between 0 and 1, where values close to 0 indicate an equal contribution of species to maintaining natural capital integrity, while values close to 1 indicate a high uniqueness contribution of species in sustaining natural capital integrity (Figure 2B).



Species loss was simulated randomly. For each level of species loss, the number of simulations correspond to approximately 70% of the total number of species, rounded to the nearest whole number.

Biological Natural Capital Resilience is defined as the minimum percentage of Biological Assets that sustain at least 95% of Natural Capital Integrity

Species loss was simulated to identify the **community composition that results in the lowest FRic at each level of species loss**. The resulting **decay curve** represents the worst-case scenario for species loss in terms of Natural Capital Integrity

Decay curve (A) represents the **worst-case scenario for species loss** in terms of Natural Capital Integrity

The Decay curve (B) represents a hypothetical scenario assuming **equal contribution of all species** to Natural Capital Integrity

The difference between area of the two scenarios (C) represents the portion of Natural Capital Integrity that is **maintained due to the uniqueness of the species that compose the community**

Biological Natural Capital Uniquiness is the portion of Natural Capital Assets underpinned by species uniqueness

Figure 2. Metrics of Biological natural capital Resilience and Uniqueness. Top: Resilience is the minimum proportion of species loss that still maintains 95% of natural capital integrity (82.2% in this example). Bottom: Uniqueness measures functional integrity loss under the worst-case species loss scenario (blue) versus equal contribution scenario (pink). The purple area (C) quantifies the integrity attributed to unique species.

Results

We constructed indices of resilience and uniqueness of natural capital supported by biodiversity based on woody plants, bees, frugivorous butterflies, and songbirds. Our dataset comprises a total of 3642 specimens, including 1886 woody plants, 154 frugivorous butterflies, and 1580 bees. Additionally, we recorded 4895 birdsongs. The total of 667 species sampled includes 287 woody plant species, 259 bird species, 54 butterfly species, and 121 bee species.

For taxonomic groups, the BNCR index, was higher in woody plants (83.6%), followed by bees (83.3%), frugivorous butterflies (80.2%), and birds (69.05%), while the multi taxa analysis of BNCR showed the highest value of resilience (89.55%; Figure 3).

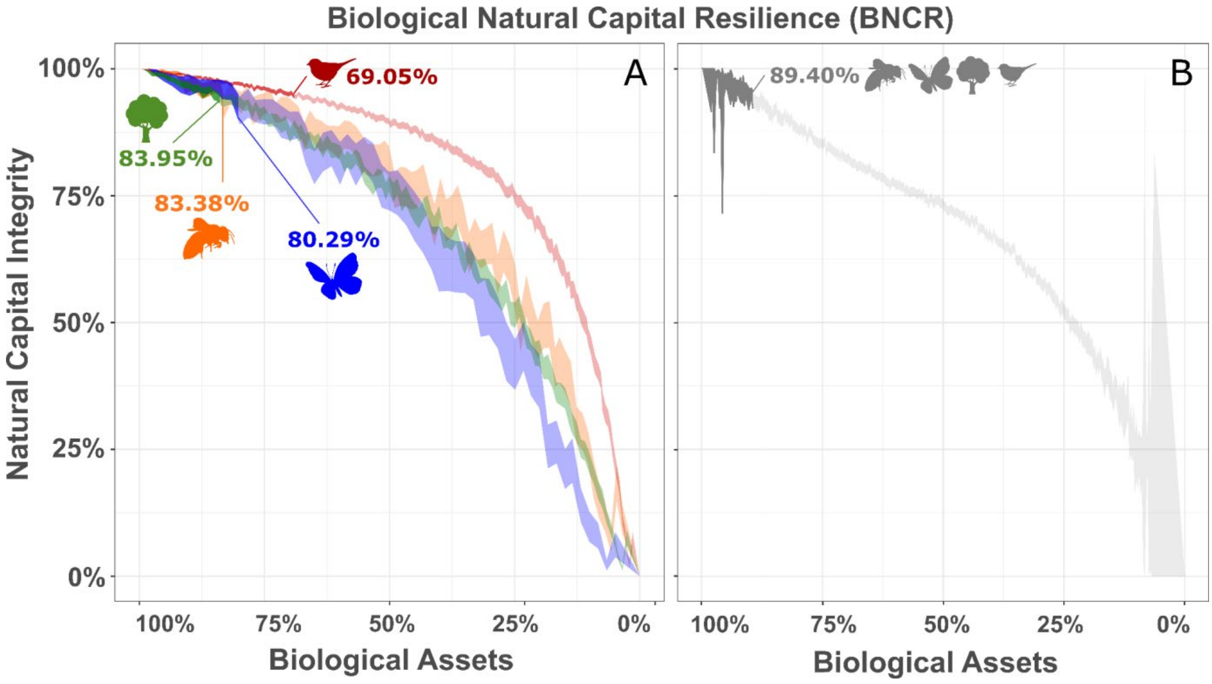


Figure 3. The biological natural capital resilience (BNCR). For each taxonomic groups (A) and multi taxa (B). In each graph, colored polygons indicate the range of the percent natural capital integrity maintained by communities with a random simulated percentage of biological assets loss. Dark colored polygons indicate communities that maintain at least 95% of the natural capital integrity, while light colored polygons indicate communities that maintain less than 95% of the natural capital integrity. The percentage indicated in each graph and the boundary between light and dark polygons indicate the minimum percentage of biological assets that sustain 95% of the natural capital integrity, named Biological natural capital Resilience (BNCR).

For BNCU, the frugivorous butterflies were the biological group with the highest BNCU index value (64.2%), followed by bees (59.2%), woody plants (59.1%) and birds (46.2%) (Figure 4).

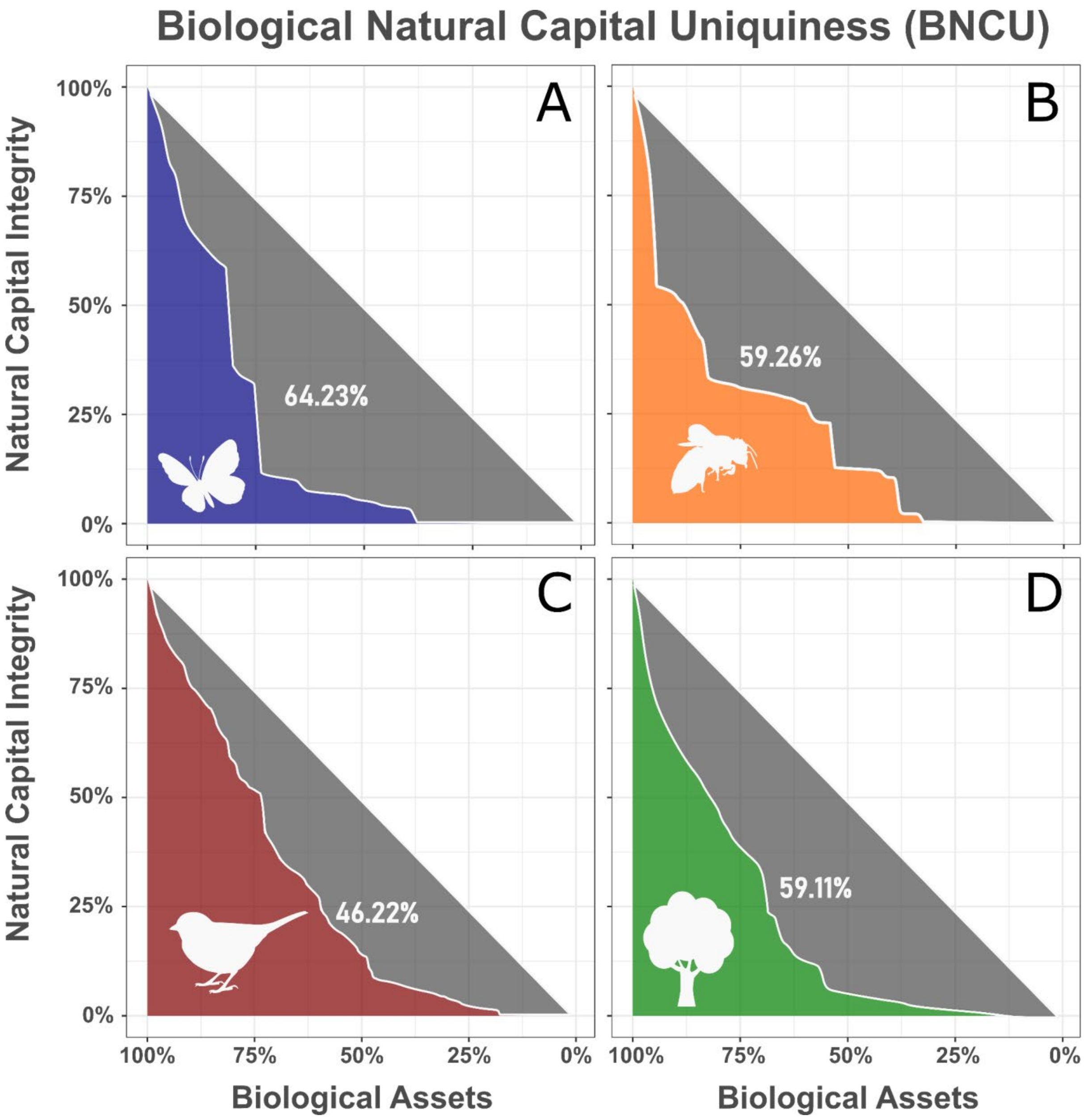

Biological Natural Capital Uniquiness (BNCU)
A
B
C
D
64.23%
59.26%
46.22%
59.11%
Natural Capital Integrity
100%
75%
50%
25%
0%
Biological Assets
100%
75%
50%
25%
0%

Figure 4. The biological natural capital uniqueness (BNCU) of the four taxonomic group. Frugivorous butterflies (A), bees (B), birds (C) and woody plants (D). In each graph, the colored polygon represents the decay curve of biological assets in the worst-case scenario of loss of integrity of natural capital, while the gray triangle (part covered by the colored polygon) represents the decay curve of biological assets in a scenario where all species contribute equally to the integrity of natural capital. Gray polygons represent the difference between the two scenarios, and its percentage in relation to the total area of the gray triangle (expressed numerically in the graph), reflects the portion of natural capital that is maintained by the unique contribution of species (BNCU).

Discussion

Our findings show that both resilience and uniqueness metrics reveal critical patterns about how biodiversity supports natural capital. BNCR values were consistently high across taxonomic groups, supperting our prediction that natural capital in these systems are mainly underpinned by biodiversiy, and that most biological assets need to be maintained to conserve natural capital integrity. Also aligned to our hypothesis, BNCU values were also elevated, indicating that a substantial portion of natural capital integrity relies on a relatively high number of unique species, expressing the high irreplaceability of many species within the studied communities. These results indicate limited functional redundancy among species, confirming our expectation of high uniqueness and showing that the loss of just a few species leads to an abrupt decline in natural capital integrity. Importantly, rather than offering generalized patterns for the entire Amazon biome, the study provides ecologically meaningful insights for the focal region and a replicable framework for other biodiversity-rich areas. These outcomes underscore the value of incorporating trait-based biodiversity measures into conservation frameworks, particularly those focused on assessing natural capital. Ultimately, the observed BNCR and BNCU values across distinct taxonomic groups indicate that the integrity of natural capital relies heavily on preserving both the quantity and the uniqueness of biological assets. These metrics provide a relative assessment of resilience and irreplaceability, highlighting that even small losses of unique species may disproportionately affect natural capital integrity.

BNCR values varied among taxonomic groups, reflecting ecological and functional differences inherent to each group. Woody plants exhibited the highest BNCR (83.95%), followed closely by bees and butterflies, while birds had the lowest (69.05%). These differences likely stem from a combination of factors, including trait composition, species richness, and ecological roles. For instance, woody plants, shaped by diverse ecological adaptations to environmental pressures such as drought and nutrient variability, exhibit a wide range of functional traits that make their contributions to ecosystem integrity unique (Swenson et al. 2012, Rossel et al. 2022),reflected in the high BNCR value, where even small losses in biological assets can disproportionately impact ecosystem stability. Similarly, Bees and butterflies, especially due to their species-level specialization in foraging and resource partitioning, such as the reliance of butterflies on distinct host plants or habitats, showed high BNCR values, reflecting a strong dependency on multiple functionally distinct species to sustain key ecological processes (Ye et al. 2024, Ramos et al. 2021). In contrast, birds, particularly in species-rich tropical regions, often exhibit high functional redundancy, wherein many species share overlapping traits and ecological roles, allowing key ecosystem functions to be maintained even if some species are lost, which is reflected in their comparatively lower BNCR values (Cooke et al. 2019, Jarzyna et al. 2021).The multitaxa BNCR exhibited the highest functional resilience value, suggesting that integrating multiple taxonomic groups may reveal greater vulnerability of the overall system. This pattern likely reflects emergent properties of ecosystem resilience, supporting previous calls for multi-taxa analyses to fully understand ecological vulnerability (Capdevila et al 2021, Seddon et al. 2021). Differences in trait composition, redundancy, and species richness among groups can reduce apparent redundancy when combined, while integrating multiple ecological scales highlights the disproportionate impact of losing highly unique species (Fischer & de Bello 2023) . Part of the high value may also reflect the large sample size and standardization across groups, which allows meaningful comparisons but can influence absolute percentages (Dalerum et al 2012).

BNCU values revealed that a considerable share of natural capital integrity relies on a relatively small subset of highly unique species. This index simulates a worst-case scenario in which species are lost sequentially from the most functionally distinct to the least, an unlikely but critical lens for assessing ecological vulnerability. Under this pessimistic assumption, ecosystem functions degrade rapidly, as the initial species lost are precisely those contributing the most unique functional roles. Our results show BNCU values ranging from 46.2% in birds to 64.2% in frugivorous butterflies, underscoring significant variation in functional distinctness among groups. Frugivorous butterflies likely exhibit high functional distinctness due to unique adaptations feed and flight shaped by environmental filters along gradients (Henriques et al. 2022). These adaptations reflect their specialization to specific habitat conditions and resource availability, making some species disproportionately important for maintaining natural capital integrity, as captured by their high contributions to the BNCU index. Similarly, bees showed high BNCU values, reflecting strong species-level specialization in foraging and pollination interactions (Mokkapati et al. 2024). In contrast, birds exhibited the lowest BNCU, reflecting the high functional redundancy typical of tropical assemblages, where many species share similar ecological roles. This pattern may arise from dense niche packing and substantial trait overlap, meaning that increases in species richness do not necessarily translate into broader functional diversity (Pigot et al. 2016, Cooke et al. 2019). As a result, the loss of even functionally distinct bird species may be partially buffered by the presence of ecologically similar species, leading to a more gradual decline in natural capital integrity. Woody plants had intermediate BNCU values, likely reflecting a balance between high species richness, which can lead to functional redundancy, and the presence of species with distinct traits that contribute uniquely to ecosystem functioning in tropical environments (Sun et al. 2024).The decay curves derived from BNCU simulations highlight the steep consequences of losing unique species: a 25% loss in biological assets led to declines of up to 88.5% in natural capital integrity. This reinforces the need to preserve functionally irreplaceable species, as their loss triggers rapid functional collapse. Importantly, functional uniqueness offers a complementary perspective to richness-based conservation, allowing the identification of species whose marginal contributions to ecosystem functioning are disproportionately high. Thus, BNCU provides a valuable framework not only for estimating worst-case functional loss, but can also informing conservation prioritization by quantifying each species' irreplaceability within the natural capital system.

Integrating functional diversity into natural capital accounting addresses a key limitation of traditional methods, which often rely solely on taxonomic diversity and overlook the varying contributions of species to ecosystem function. Functional traits offer a process-based perspective, emphasizing the roles species play in key ecosystem processes such as nutrient cycling, productivity, and resilience. Our approach, aligned with recent calls to incorporate these dimensions (Mace et al. 2019; Ricotta et al. 2016), employs interpretable metrics (BNCR and BNCU) that are applicable at local or regional scales without requiring reference areas. By converting functional diversity metrics into measures of natural capital, our approach allows for a more direct accounting of how biodiversity supports ecosystem services, by selecting functional traits related to these relevant ecosystem services (for example, wood density for timber production, or bee proboscis length for flower reproduction). An essential step in a functional approach involves the careful selection of functional traits, taking into account the specific ecological processes, services, and responses to which these traits are related (Violle et al., 2007). This represents an opportunity for a targeted functional approach to natural capital accounting, as it allows for the selection of traits associated with ecosystem services and highly valued benefits, as well as those that indirectly support ecosystem services and processes that are difficult to express in monetary terms (Mace et al., 2019). It is particularly important, especially in a multi-taxon approach, to carefully consider the number, resolution, and nature of functional attributes, aiming for a balanced representation across taxonomic groups. In this regard, we also recommend analyzing metric sensitivity to functional traits (Supplementary Information IV). For example, the relatively low BNCR values of birds may partially result from coarser trait resolution in global databases. Whenever possible, we recommend using locally collected, high-resolution traits, which better capture functional variation and improve the accuracy and interpretability of functional diversity metrics.

Another valuable advantage of the proposed approach lies in its relevance beyond traditional diversity measures. The indices used are ecologically meaningful and easily interpretable within the context of natural capital - expressing both the percentage of biological assets required to sustain natural capital and the proportion of capital supported by the uniqueness of these assets - enhancing their integration into broader natural capital frameworks, bridging ecological insight with economic valuation. Their expression as percentages also allows assessment of a single area independently, without requiring external comparisons. In this context, it is important to interpret BNCR and BNCU values within a relative framework rather than relying on absolute thresholds. For BNCU, a conceptual reference scenario corresponds to a community where all species contribute equally to ecosystem functioning, similar to assumptions made by species-richness based metrics. Values deviating from this scenario indicate elevated functional uniqueness. For BNCR, however, no neutral scenario exists: when species are not functionally redundant, any loss of species proportionally reduces functional richness, making high or low BNCR inherently context-dependent. Thus, “high” or “low” values are interpreted relative to the observed patterns within each community, allowing us to assess the resilience and vulnerability of natural capital in a descriptive and methodologically meaningful way. It is important to note that accurate interpretation of these indices also depends on sufficient sampling completeness, as incomplete surveys may underestimate functional richness or uniqueness, and assess sampling coverage (Supplmentary Information I) ensures that pooled communities reasonably represent the local species pool, increasing confidence in the derived BNCR and BNCU values. Despite these advantages and the benefits of standardization, it is essential to be cautious when comparing values across taxonomic groups or regions. While natural capital accounting is primarily designed for spatially explicit assessments of ecosystem stocks and service flows within defined territories (Hein et al. 2020; Arguillo et al. 2022), it can also be used to compare natural capital across regions under specific conditions. Such comparisons require standardized and ecologically meaningful metrics, consistent data quality and taxonomic resolution across sites, and harmonized definitions of ecosystem boundaries and functional units (Maechler & Graz 2020).

Our study demonstrates that the proposed metrics, BNCR and BNCU, effectively capture critical dimensions of ecological resilience and species uniqueness within the natural capital framework. The variation observed among taxonomic groups likely reflects underlying ecological filters and evolutionary adaptations that shape species’ functional traits and roles. This variation allows the approach to differentiate groups that are more or less susceptible to biodiversity loss and functional decline, providing nuanced insights into community vulnerability. Importantly, adopting a multitaxa perspective reveals the compounded fragility of natural capital integrity when multiple taxonomic groups are considered together, emphasizing the need for integrative conservation efforts that transcend single-taxon focus. The BNCR and BNCU metrics complement each other by quantifying both the resilience of ecosystem functions to species loss and the irreplaceability of unique functional contributions, respectively. Their standardized and interpretable nature enables their incorporation into natural capital accounting, bridging ecological theory with applied management. By integrating functional diversity into natural capital assessments, this approach expands the scope beyond traditional taxonomic measures, which often underestimate the value of biological assets. This opens opportunities to include a wider array of functional traits and other biological assets, providing a more realistic and comprehensive valuation of natural capital. Ultimately, embedding functional ecology within natural capital frameworks supports more informed and adaptive biodiversity conservation and land-use planning. It enables prioritization strategies that consider not only species richness but also the functional roles critical for ecosystem resilience and sustainability, advancing the integration of ecological complexity into natural capital management and policy.

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Author contributions

Felipe Martello and Tereza Cristina Giannini conceptualized the research; Felipe Martello and Tereza Cristina Giannini, Caroline Oliveira Andrino; Rafael Gomes Barbosa-Silva; Amanda Paracampo; Rafael Cabral Borges; Ulysses Madureira Maia; Sidnei M. Dantas and Leonardo de Sousa Miranda conducted the investigation; Tereza Cristina Giannini supervisioned the research, Felipe Martello and Tereza Cristina Giannini wrote the main manuscript; Caroline Oliveira Andrino; Rafael Gomes Barbosa-Silva,Ulysses Madureira Maia, Rafael Cabral Borges, Daniela C. Zappi, Marina Zanin, Leonardo de Sousa Miranda, Jesus Aguirre-Gutierrez and Yadvinder Malhi reviewed and edited the manuscript.

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The authors declare that there are no conflicts of interest

Data availability statement

Data available from the Oxford University Research Archive repository (ORA)
https://ora.ox.ac.uk/objects/uuid:a2ee43d8-9fef-47fd-87f4-8f672e591e8c
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