

RESEARCH ARTICLE

Multi-Taxa Responses to Climate Change in the Amazon Forest

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ABSTRACT

Tropical biodiversity is undergoing unprecedented changes due to the hydrological cycle intensification, characterized by more intense droughts and wet seasons. This raises concerns about the resilience of animal and plant communities to such extremes and the existence of potential refugia—areas theorized to safeguard biological communities from adverse climate impacts. Over 20 years of monitoring in Central Amazonia, we investigated the short-term and long-term effects of hydrological cycle intensification on bird, fish, ant, and palm communities. We explored whether the ‘insurance effect’ of climate trends (droughts buffered by preceded wet seasons) or ‘environmental refugia’ (droughts or floods buffered by topographic features) could lessen the impact of climate events on community composition, richness, evenness, and species rank. Pronounced abundance changes were observed among animal species, whereas palm species showed relative temporal stability. Birds and fish were more affected by the immediate and long-term severity of droughts and wet periods, while ants responded primarily to short-term drought impacts. Conversely, palm communities exhibited delayed responses to climate extremes, primarily in long-term comparisons. As expected, the proposed ‘insurance effect’ mitigates the long-term impacts of extreme climate events on animal and plant community trends. However, less extreme hydrological conditions linked to topographic features did not provide effective ‘environmental refugia’ for animals or plants during adverse climate conditions. These outcomes underscore the complex and varied biological responses to ongoing climate change, challenging the

1 | Introduction

Extreme climatic events severely affect human activities and reshape tropical forests (Malhi et al. 2014). In Amazonia, where the world's largest tropical forest is located, there has been an intensification of hydrological cycles with more intense droughts and wet seasons related to Tropical Atlantic warming, Pacific cooling (Barichivich et al. 2018), and El Niño/La Niña Southern Oscillation (Gloor et al. 2013). Such extremes repeated over time are expected to create 'novel' climate conditions, influencing local demographic processes and the long-term viability of species populations (Carcia et al. 2014), potentially accelerating the formation of new ecological communities (Blowes et al. 2019). The uncertainty about the responses of local communities to climatic extremes, along with projected rainfall changes, raises concerns for the future of tropical biodiversity.

Climate extremes lead to highly variable temporal trends in biodiversity at local scales (Evans et al. 2022; Stouffer et al. 2021). This variation suggests that unknown factors may modulate the direct effects of climate change on biodiversity, potentially amplifying or mitigating these effects locally. For example, cooler, more humid mountain tops or isolated patches of vegetation in deserts can relieve extreme temperatures and water deficits, acting as natural refugia for biodiversity (McLaughlin et al. 2017). Such refugia against climate extremes have also been identified in humid microhabitats, which buffer the impacts of prolonged droughts on Australian bird populations by providing moisture and scarce food resources in drier areas (Selwood et al. 2015). Additionally, periods when climatic conditions are less extreme also offer opportunities for species to persist over time (Costa et al. 2022). In the Amazon forest, there is evidence of a complex 'insurance effect' mechanism for trees. For instance, during the severe 2015–2016 drought, the trees experienced low mortality and high growth because the preceding years of 2013–2014 were marked by unusually intense rainfall, likely creating a water reserve in the soil and groundwater that mitigated the negative impact of the extreme drought (Esteban et al. 2021). Therefore, in different ecosystems, certain environmental patches or special arrangements of climatic events along time periods could minimize the impact of climate extremes on biodiversity through environmental refuges or 'insurance effect' mechanisms. Identifying these critical spatial and temporal conditions is essential for conservation efforts, as they offer a safer buffer for biodiversity against climate extremes.

The 'insurance effect' concept is a potential mechanism to account for climate-biodiversity relationships. This insurance would emerge from the groundwater memory, which is established when periods of extreme rainfall (wetness) precede droughts (Tomasella et al. 2008), potentially mitigating the negative impacts of droughts on biological communities. This mechanism involves recharging groundwater reserves, amplified during extreme rainfall due to the increased water

infiltration (Tomasella et al. 2008). The stored groundwater responds slowly and gradually to rainfall, ensuring continuous release to the soil and water bodies during droughts. This delayed hydrological response enhances soil moisture and maintains stream flow, mitigating the adverse effects of dry spells (Miguez-Macho and Fan 2012b). For aquatic organisms, sustained stream flow during droughts can prevent habitat loss and maintain water quality (Borba et al. 2021), while for terrestrial organisms, enhanced soil moisture can alleviate water stress, reduce plant mortality, and support the overall stability of the ecosystem (Esteban et al. 2021; Sousa et al. 2020). A trend towards increased annual precipitation has been noted in Central Amazonia (3.5 mm year^{-1} since 1966; Figure S1), leading to frequent 'wet then drought' scenarios, which are expected to reduce the impacts of droughts on temporal biodiversity changes.

Local topographic variation can modulate biological community resilience under extreme climates, determining the portions of the forest that would be environmental refuges (McLaughlin et al. 2017). In Central Amazonia, elevated areas with well-drained soils are vertically distant from groundwater sources, while lower areas are often moister and water-saturated (Rennó et al. 2008). These topographical differences can create microclimate refugia during extreme climatic events. In terrestrial environments, water deficits more severely impact plateaus and ridges due to limited water availability, potentially increasing plant mortality (McDowell et al. 2008) and indirectly affecting fauna. Conversely, lowlands and valleys often maintain higher soil moisture, reducing water deficits (Costa et al. 2022). However, these areas may suffer from waterlogging and anoxia during periods of water excess, leading to plant mortality and reduced soil volume to soil fauna (Baccaro et al. 2013; Sousa et al. 2022). In aquatic environments, smaller streams are highly susceptible to discharge disturbances after local rainfalls, while larger streams with increased size and sinuosity potentially lessen the effects of extreme rains (Borba et al. 2021). These topographic features may buffer the impact of extreme climatic events on biodiversity, depending on the portion of the topographic gradient in which the species occurs and its intrinsic features.

Plant and animal groups vary in features that could determine their higher or lower sensitivity to climate change and the speed of its impact on each assemblage. The magnitude of the impact of climate change could be explained by differences in the life history strategies of these groups (e.g., generation time and longevity, dispersal limitation; Compagnoni et al. 2021). Taxa with shorter generation times, such as many invertebrates and some small vertebrates, may respond rapidly to climate extremes, leading to immediate shifts in species composition, abundance, and richness (short-term trends; Evans et al. 2022). In contrast, taxa with longer lifespans, such as most palms and trees, exhibit more gradual changes that become evident only over time, reflecting the long-term effects of multiple extreme climate events (Costa et al. 2020;

Esquivel-Muelbert et al. 2019). Although we have expectations associated with the lifespan of these groups, we know very little about the differential impact of extreme events on different taxa under the same local environmental conditions and whether they could broadly benefit from the ‘insurance effect’ of certain environmental refuges. Comparative analyses across plant and animal communities can test these predictions, helping to clarify how different taxa respond to or are buffered against extreme climate events.

Long-term monitoring of animal and plant communities encompassing extreme climatic events is vital for understanding the impacts of climate change on biodiversity. The Long-Term Ecological Research Site (LTER) in *Reserva Florestal Ducke* (RFD) in Central Amazonia is ideal for such studies (Costa et al. 2020). The preserved reserve allows a focused examination of climate effects on biodiversity without confounding factors such as land-use changes or a spatially varying climate. In this study, we explored the direct and interactive effects of two extreme climatic events (water excess and water deficit) across a mesoscale hydro-topographic gradient. Given differences in life history strategies, we expect animal communities to respond more rapidly to these climate extremes than plant communities, which may show more gradual changes over time. More specifically, we test two not mutually exclusive hypotheses: (1) The ‘Insurance effect’ hypothesis posits that the severity of wetness preceding droughts mitigates their impact, leading to less pronounced shifts in community composition—including richness, evenness, and species rank—than expected under drought conditions alone; and (2) The ‘Environmental refugia’ hypothesis posits that some positions along the hydro-topographic gradient are less susceptible to climate extremes. Thus, the effects of extreme droughts are expected to be lower in lowlands than in plateaus and ridges, while the effects of extreme wet periods are expected to be lower in plateaus and ridges than in lowlands. Additionally, droughts and wet periods would promote larger biodiversity changes in smaller streams than in larger ones.

2 | Materials and Methods

2.1 | Study Area and Rainfall Regime

The data used in this study were collected at the *Reserva Florestal Ducke* (RFD) near Manaus, Brazil, from 2001 to 2023. This protected area is part of the Long-Term Ecological Research Program (LTER) and stands out as the unique location in central Amazon where systematic standardized multi-taxa (e.g., birds, fish, ants, and palms) monitoring has been conducted together on the same plots over 20 years. The RFD covers approximately 10,000 ha (100 km²) of largely undisturbed old-growth *terra firme* rainforest and encompasses an elevation range of 39 to 140 m above sea level. The reserve features a central plateau separating two drainage basins, one flowing into the Negro River and the other into the Solimões-Amazonas River. The streams range from first to fourth order, encompassing diverse substrate types and water velocity conditions (Mendonça, Magnusson, and Zuanon 2005). The mean annual rainfall at RFD over the last 58 years (1966–2023) is 2572 ± 351 mm, with an increasing trend of 3.5 mm per year, highlighting significant

shifts in Amazonian rainfall patterns since the 2000s (Marengo et al. 2018).

2.2 | Biological Monitoring

Biological monitoring was carried out in 31 terrestrial and 26 aquatic permanent plots (Figure 1a; Table S1). The plots of terrestrial groups (birds, ants, and palms) were strategically located along altitudinal isolines to minimize altitude and soil variations within each plot. Aquatic organisms (fish) were monitored in plots encompassing streams of first and second order within the RFD (Borba et al. 2021).

Here's an overview of our sampling methods for different groups (see Figure S2 for how sampling was done within each aquatic or terrestrial plot):

2.2.1 | Birds

Bird species were captured in 30 permanent plots using 15 mist nests (10 m long) in each plot. Nets were installed in pairs plus a single net, placed 10 m apart from each other along the plot. These nets were open from 06:00 to 12:00 and checked every 40 min. Captured birds were identified and banded with metal bands, and this procedure occurred once during each sampling period.

2.2.2 | Fish

Fish monitoring was carried out in 26 permanent aquatic plots located along first- to second-order streams, classified according to the Strahler system (Strahler 1957). These plots covered a 50 m long stream section and were identified based on the Igarapés project records (<https://ppbio.inpa.gov.br/sites/default/files/Peixes.pdf>, Mendonça, Magnusson, and Zuanon 2005).

2.2.3 | Ants

Ant species were sampled in 30 permanent plots using 10 pitfall traps placed along the 250 m length of each plot. Each trap, approximately 9.5 cm in diameter, was partially filled with a solution of 70% alcohol with a drop of neutral detergent and left open for 48 h. Ant samplings were conducted exclusively during the dry season between August and October.

2.2.3.1 | Palms. Palm species were sampled in 13 permanent plots of 250 m in length and with varying widths based on palm sizes: 4 m with 1–10 cm diameter at breast height (DBH), 20 m for those with 10–30 cm DBH, and 40 m for over 30 cm DBH. Palm species were measured following Condit's (1998) directions adapted for RAPELD plots, as detailed in the online sampling protocol (https://ppbio.inpa.gov.br/sites/default/files/Protocolo_estrutura_vegetacao_2014_0.pdf). Each plant was tagged during every census to ensure data accuracy.

All individuals sampled or recorded were identified at the species level whenever possible. When species delimitation was

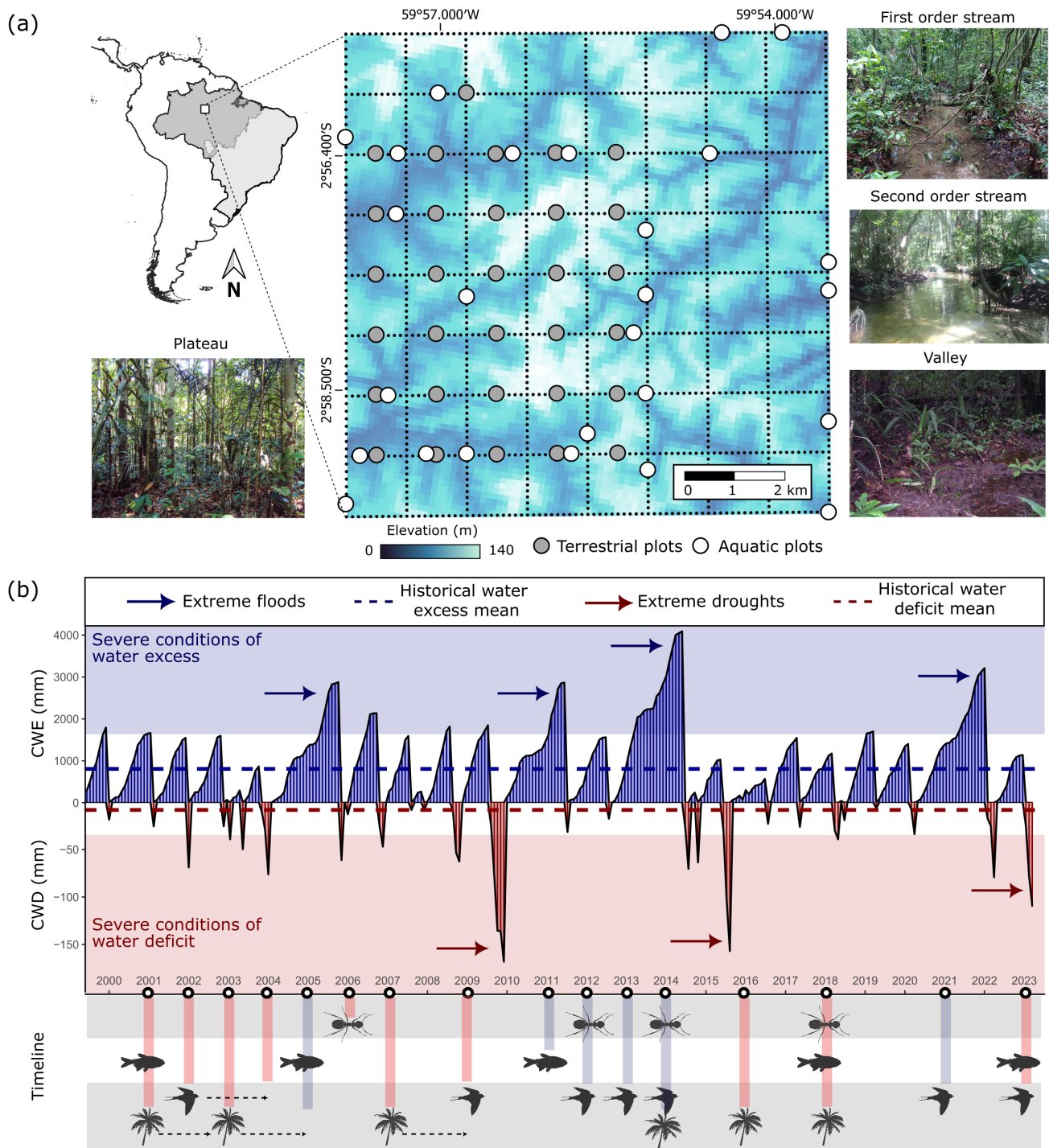


FIGURE 1 | (a) Location of terrestrial (grey circles) and aquatic (white circles) plots sampled for long-term monitoring in the Reserva Florestal Ducke, Amazonia. (b) Cumulative water deficit (CWD) and cumulative water excess (CWE) from 2000 to 2023. Density curves indicate periods of water excess (blue) and water deficit (red) conditions during the study period, with extreme climatic events represented by blue (highest positive WEI index) and red arrows (highest negative WDI index). The timeline for each biological group is shown at the bottom, with vertical bars expressing if the sampling was carried out in years characterized by drought (red) or wetness (blue). Dashed arrows indicate sampling that began in 1 year and ended in another, as observed for birds and palms (Table S1). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

impossible, we assigned the same morphotype code across all sampling plots and rounds. This sampling standardization resulted in 41% of morphotypes of ants (119 species), 5% of fish (three species), and 5% of palms (one species). All understory birds were identified at the species level.

2.3 | Hydro-Topographic Gradient and Climate Variables

Local hydro-topographic conditions were characterized by the height above the nearest drainage (HAND) for terrestrial plots

(Rennó et al. 2008) and stream order for aquatic plots. HAND, calculated from normalizing elevation data derived from a digital elevation model (DEM) to the nearest drainage, links topography to soil hydrology (Rennó et al. 2008; Schietti et al. 2013). High HAND values indicate greater drainage potential, while low values suggest proximity to the water table, where water can accumulate and lead to waterlogged conditions (Nobre et al. 2011).

To quantify precipitation extremes, expressed as rainfall deficit or excess severity, we used well-established indices of cumulative water deficit (CWD; Aragão et al. 2007) and water excess (CWE; Esteban et al. 2021), utilizing a long-term local climate record of rainfall from the RFD meteorological station. The RFD meteorological station has been collecting rainfall data since 1966. CWD measures drought severity from precipitation records as follows:

$$CWD_n = CWD_{n-1} + PP_n - ET_n$$

where n represents month, PP_n represents the monthly precipitation, and ET_n represents the monthly evapotranspiration, assumed to be 100 mm per month (due to the nearly constant evapotranspiration rate of moist tropical canopies; Rocha et al. 2004). Therefore, the deficits are negative numbers, with lower values of CWD_n representing more severe droughts. If CWD_n exceeds zero in a given month, the excess water is assumed to be runoff, and the CWD_n for that month is reset to zero. Therefore, CWD_n is always less than or equal to zero for all months. Conversely, to express the severity of wetness, we calculated the monthly cumulative water excess (CWE) using a logic inverse to that of CWD. For months without water deficit ($CWD=0$), the value of CWE is set as the volume of PP of that month minus the monthly ET (100 mm). The CWE for the subsequent month is calculated similarly but adds the CWE from previous months. Studies show that runoff contributes less than 10% of stream and river discharge in Amazonian forests (reviewed in Miguez-Macho and Fan 2012a). With evapotranspiration factored in and runoff losses generally small, most of the excess rainfall (CWE) will recharge the soil and subsequently the groundwater (Tomasella et al. 2008).

Based on this long-term record of CWD and CWE, consisting of 612 monthly values (51 years) for both metrics, we calculated their historical mean and standard deviation (SD) to characterize climate anomalies during our study period (2001–2023). We then calculated the index of water deficit (WDI) and water excess (WEI) for each month. The WDI was calculated by summing monthly CWD values that exceeded one SD from the mean historical CWD. Only monthly CWD values exceeding one SD were considered to ensure we captured severe conditions (anomalies). Owing to variation in measurement intervals between sampling, we standardized the SD sum of CWD anomalies by the duration of the sampling interval (number of months) to ensure comparability of WDI values across all intervals. Thus, the WDI for each sampling interval was calculated as:

$$WDI = \sum_{i=1}^n \frac{CWD_i}{n}; CWD_i > CWD_{SD}$$

where CWD_i is the cumulative water deficit for month i , n is the number of months within the sampling interval, and CWD_{SD} is the sum of the mean historical CWD plus one SD (1966–2023).

Similarly, the water excess index (WEI) was calculated as the sum of monthly CWE values divided by the number of months within each interval. The following analyses treated the WDI and WEI as a proxy for rainfall extremes.

2.4 | Quantifying Biodiversity Trends

We evaluated biodiversity trends for each taxon using species composition dissimilarity and community component metrics (richness, species rank, and evenness) to track changes in species identity and richness. To achieve this, we employed two approaches to capture temporal changes in these metrics.

The first approach focused on patterns between biodiversity sampling periods, comparing consecutive sampling periods (e.g., from sampling 1 to sampling 2, sampling 2 to sampling 3, and so on). Investigating temporal changes across consecutive sampling events captures snapshot changes in biodiversity that might be driven by specific extreme climate events, which we define as a short-term comparison (Garcia et al. 2014). This approach highlights immediate responses and fluctuations within shorter intervals (~3.6 years in our entire dataset; Table S1). Complementarily, the second approach focused on changes in biodiversity over the sampling period relative to the first sampling, using the first sampling as the baseline and comparing all subsequent samplings to it (e.g., from sampling 1 to sampling 2, sampling 1 to sampling 3, and so on; Dornelas et al. 2014). Using the first sampling event as the baseline to calculate biodiversity changes in subsequent samplings allows us to describe the trajectory of local assemblages over a more extended period (approximately 20 years, Table S1), which we define as a long-term comparison. Choosing the first year as a baseline is reasonable, given that its CWE and CWD value were far from the threshold for extreme drought conditions (the area shaded in red in Figure 1). The baseline year for ants (2006) coincided with heavy rain. Although significant, this wet period was not the most extreme event recorded during the study period (e.g., 2011 and 2014 in Figure 1). Therefore, we assume that our samplings were carried out during years that, overall, reflect relatively normal conditions in terms of precipitation patterns, minimizing the potential bias that extreme events might introduce at the start of the monitoring period.

For both short-term and long-term comparisons, we calculated the temporal dissimilarity based on presence/absence (Sørensen index) and abundance data (Bray-Curtis index) using the 'beta' function in the R package BAT (Cardoso, Rigal, and Carvalho 2015). We also examined changes in community components for each taxa considering short and cumulative approaches, using the 'RAC_change' function of the R package codyn (Avolio et al. 2019). Richness changes reflect species gains and losses, evenness changes measure the variation in the abundance distribution among species, and rank changes indicate a reordering of species abundances over time. For the latter, an extreme example would be the rarest species for a given plot in the first sampling, becoming the most abundant in the next, or vice-versa. Changes in species rank are divided by the size of the species pool, making the measure independent of species richness. Richness and evenness changes range from -1 to 1, with negative and positive values indicating decreases and increases, respectively. Rank values range from 0 to 0.5, with higher values indicating greater changes in average species rank position across sampling (Avolio et al. 2019).

2.5 | Statistical Analyses

We initially employed rank abundance curves (RAC plots) to explore species abundance changes across consecutive sampling (short-term comparison) and between the first and final sampling (long-term comparison). These plots reveal various structural aspects of communities. They are valuable for identifying shifts in species ranks, abundance distributions, and isolated occurrences (e.g., species captured in a single sampling) over time (Matthews and Whittaker 2015).

To investigate the influence of rainfall extremes and local topography on biodiversity change considering short-term and long-term comparisons, we employed linear mixed models (LMM) using the 'glmmTMB' function of the *glmmTMB* package (Brooks et al. 2017), assuming Gaussian distribution. The models assessed trends related to water deficit index (WDI), water excess index (WEI), and local hydro-topographic gradient (HAND for terrestrial, stream order for aquatic) for each taxon:

Response variable $\sim$ WDI: WEI + WDI*(HAND or Stream order) + WEI*(HAND or Stream order) + random (plot ID)

'random' represents a random intercept, accounting for autocorrelation with plot ID, and '*' includes the main effects and the interaction among them. Continuous predictor variables were standardized to mean zero and SD of one to enable direct comparison of model estimate coefficients. For instance, the 'insurance effect' hypothesis, reflecting changes in response variables where water excess precedes water deficit, was evaluated through WDI and WEI interactions (WDI:WEI). Similarly, the 'environmental refugia' hypothesis was tested via interactions between WDI or WEI and HAND or stream order, exploring how the environment modulates rainfall impacts on biodiversity.

Due to the strong correlation between WDI and WEI in ant communities (Figure S3), their models were adjusted to exclude the 'insurance effect' hypothesis. Model fit was checked via histograms of residuals and Q-Q plots, with zero-inflation addressed where necessary (see Table S2). Predictor significance was determined using Wald's statistic from LMM outputs, visualized using effect-size plots. Detailed model tables and effect sizes are in Table S2. Analyses were conducted using R version 4.2.2 (R Core Team 2023).

3 | Results

3.1 | Temporal Dynamics and Abundance Changes Among Species

During the study period (2001–2023), we observed several notable climate extremes. There were four major wet events, with the highest positive WEI indices occurring in 2005, 2011, 2013–2014, and 2021–2022 (blue arrows in Figure 1b). Conversely, three significant drought events were recorded, marked by the highest negative WDI indices in 2009–2010, 2015–2016, and 2023 (red arrows in Figure 1b). Animal species, particularly the top 10% most abundant, exhibited considerable fluctuations in abundance across these extremes, while the dominant palm species, *Oenocarpus bataua*, remained relatively stable over 17 years (short-term in Figure 2). These fluctuations in animal populations contributed to

higher temporal dissimilarity and greater abundance reordering compared to palms (Figure S4). Notably, the ant-following bird *Gymnopithys rufigula* and the large piscivorous fish *Erythrinus erythrinus* experienced declines of more than 87%, while the ant species *Crematogaster tenuicula* increased by up to 70%. These abundance trends were also reflected in rank abundance curves when considering all species (Figure S5). Additionally, single occurrences—often associated with animal species—were not limited to singletons but also included species at both the top and middle ranks of the abundance curves (triangles in Figure 2).

3.2 | Climate-Driven Divergent Trends for Animals and Plants

The hydro-topographic gradient had minimal influence on invertebrates but significantly impacted other groups. Plateaus, ridges (high HAND), and larger streams (second order) exhibited higher species richness and temporal dissimilarity compared to valleys and smaller streams (Figure 3). Notably, palm communities in plateaus and ridges experienced greater rank changes than those in valleys, indicating more pronounced community shifts in these environments (Figure 3).

Responses to water deficit (WDI) and excess (WEI) also varied among groups, with significant differences between short-term and long-term comparisons (Figure 3). For instance, increased drought severity resulted in a 26% rise in fish species richness, while ant species richness declined by up to 36%, alongside greater dissimilarity in bird communities (Figures S6–S8). In the long term, the impact of extreme events was less pronounced in ants, suggesting short-term resilience, whereas bird communities showed considerable long-term changes in species richness (Figure S6). Additionally, prolonged droughts led to more homogeneous palm communities, with reduced species reordering and temporal stability (Figure S9).

3.3 | Interactions of Water Excess and Deficit in Temporal Biodiversity Trends

The interaction between water deficit (WDI) and excess (WEI) has differing effects on birds and fish in short-term comparisons (Figure 3). For birds, extreme wet events (WEI > 0) followed by dry periods resulted in higher WDI, leading to increased temporal dissimilarity (dark blue lines in Figure 4a). In fish, however, the same pattern negatively influenced temporal dissimilarity. Conversely, when no significant excess water preceded droughts (WEI $\approx$ 0), increasing drought severity (WDI) did not lead to major compositional changes in either bird or fish communities (light blue lines in Figure 4a,b).

In the long term, the interaction of WEI and WDI consistently had negative effects on birds, fish, and palm communities, leading to decreased temporal dissimilarity and species rank change (Figure 3). For birds, when extreme wet periods were followed by drought, species dissimilarity increased with drought severity (dark blue lines in Figure 4d). The opposite pattern was observed for species richness, with richness declining under the same conditions. Meanwhile, fish and palm communities showed the reverse trend: when high rainfall (WEI > 0)

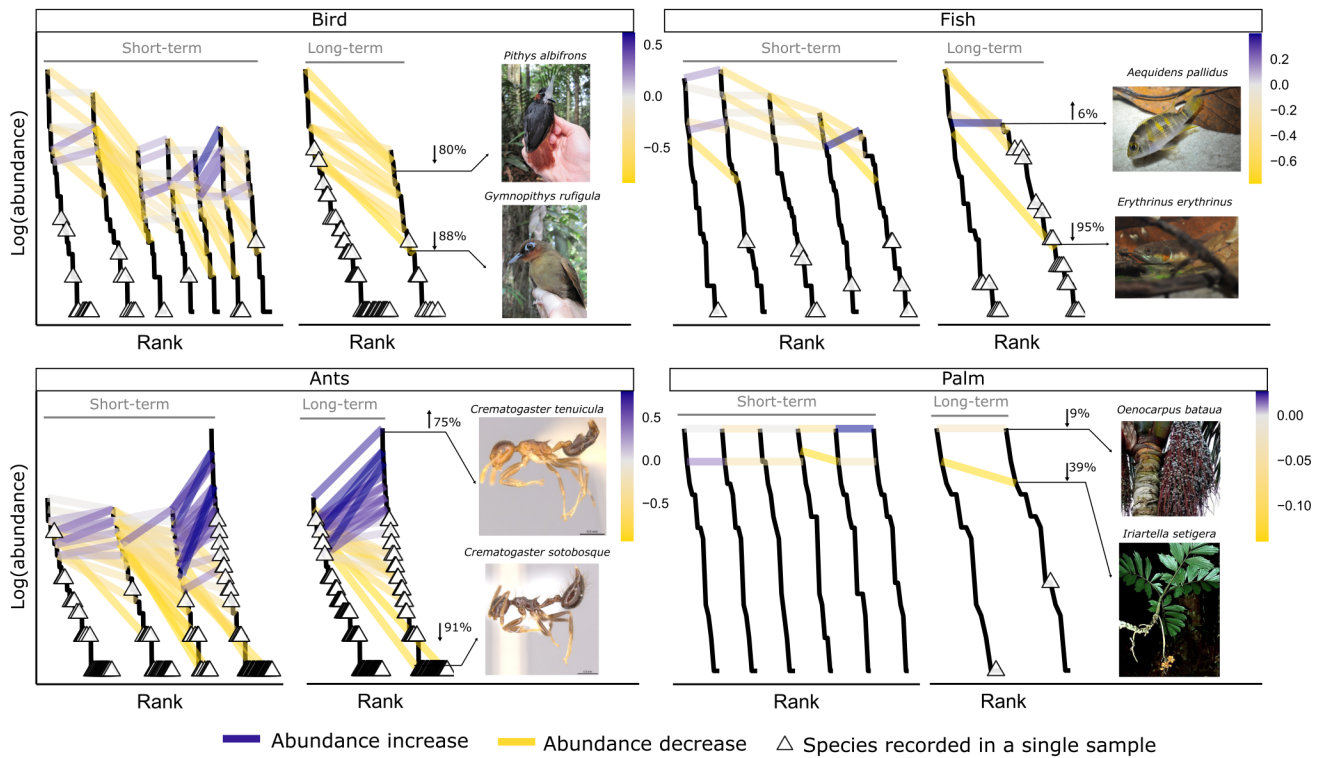


FIGURE 2 | Temporal rank abundance curves (RAC) for species of different taxa sampled in the Reserva Florestal Ducke (RFD), Amazonia, from 2001 to 2023. For each species, RACs were built to capture short-term (across consecutive sampling) and long-term (between first and final sampling) comparisons in species abundance. Each vertical line represents the species abundance rank (logarithm-based) in a different year, with the species ordered from the most to the least abundant (highest to the lowest rank). The yellow to blue color gradient represents the abundance change for the top 10% most abundant species. Triangles denote species with only a single record throughout all samplings. Photographs correspond to key species discussed in the text. Species photographs were taken by J.M., R.P.L., and I.O.F.

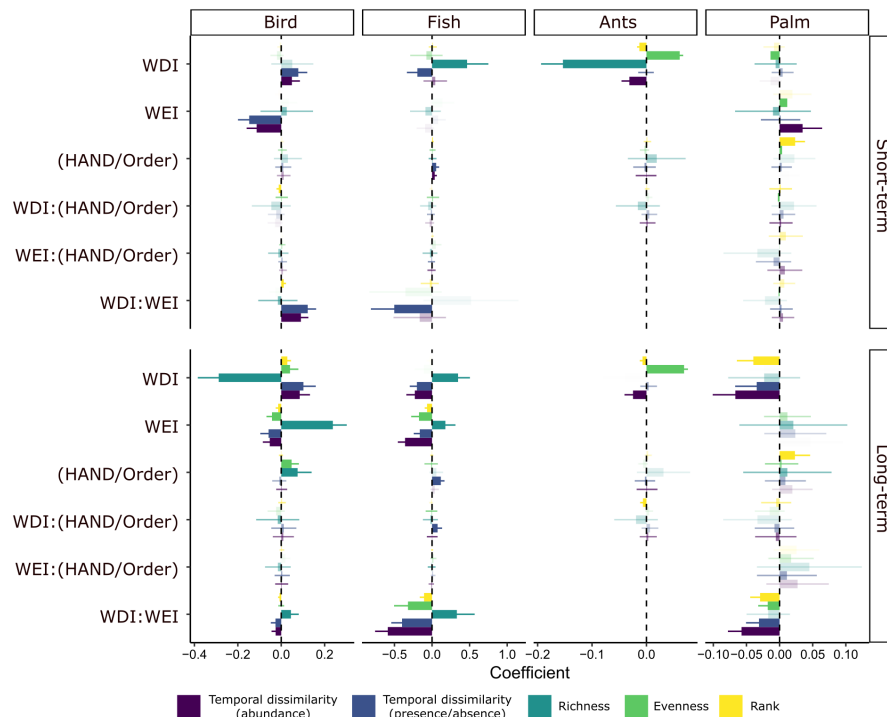


FIGURE 3 | Coefficients and 95% confidence intervals of isolated and interaction effects of the climate extremes (water deficit index [WDI] and water excess index [WEI]) and local topography (height above nearest distance, HAND, and stream order) are used in linear mixed models (LMM) to explain the short-term and long-term trends for animal and plant communities in RFD, Amazonia. Bars represent the magnitude of effect; the higher the bar, the greater the impact of extreme weather events on biodiversity changes.

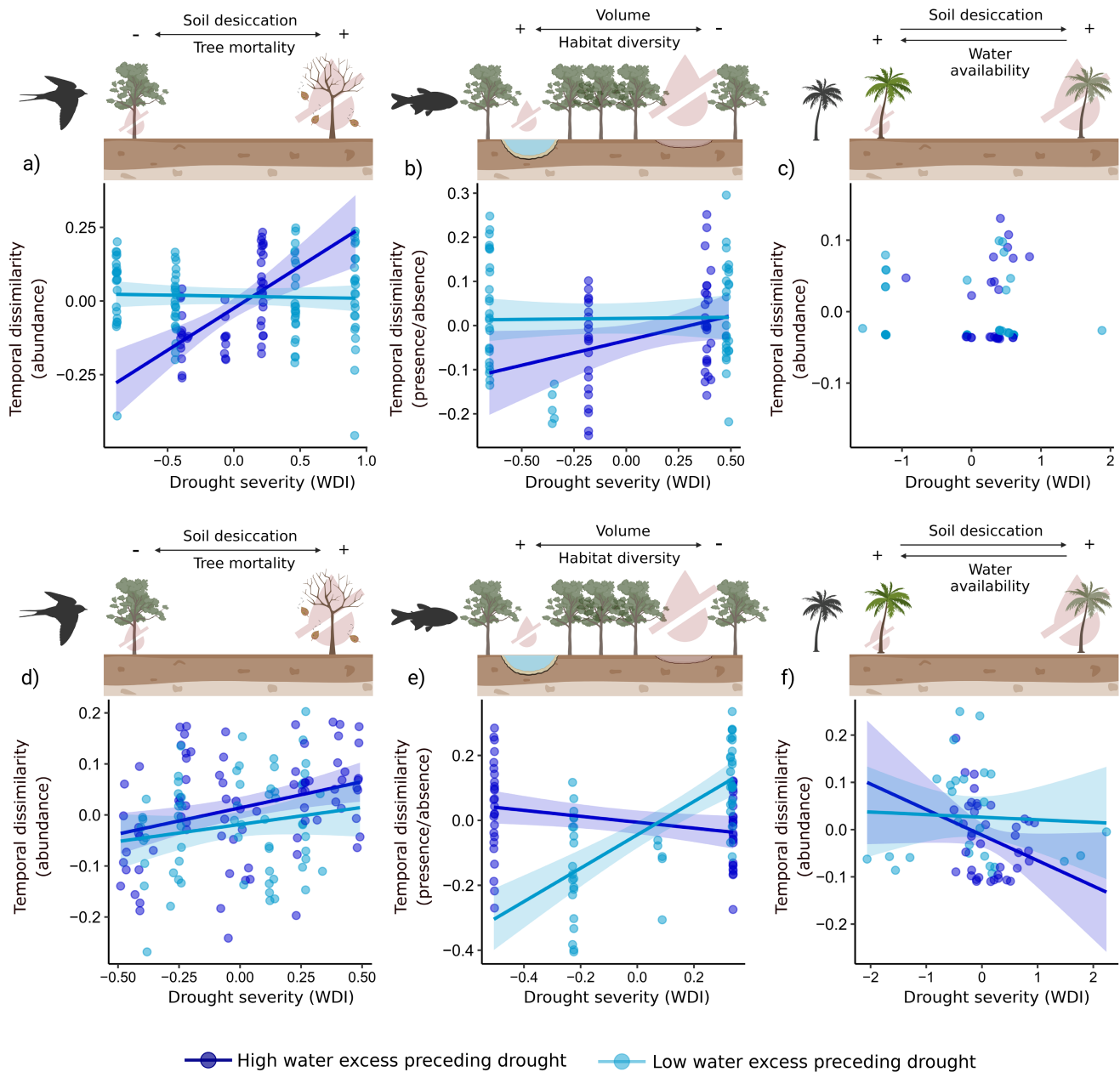


FIGURE 4 | Partial plots illustrating the interaction of wet periods with drought affecting bird, fish, and palm compositional change. Each panel depicts the gradient of habitat alteration in response to short-term (a–c) and long-term comparisons (d–f) to extreme drought severity. (a–c) When high rainfall accumulation was followed by droughts, higher drought severity increased the temporal dissimilarity of bird and fish communities (dark blue line) while not promoting significant change in palms. (d–f) In the long term, when extreme wet periods precede droughts, drought severity increases community temporal dissimilarity in birds and decreases temporal dissimilarity in fish and palms (dark blue line). Data were split into two groups based on the median WEI values for clearer representation. Lines represent the overall tendency, with shading indicating 95% confidence intervals.

preceded droughts, higher WDI decreased temporal dissimilarity (dark blue lines in Figure 4e,f), which was associated with less rank and evenness change.

3.4 | Topography Did Not Act as Refuges During Adverse Climate Conditions

In lowlands, bird communities increased rank changes with increasing drought in the short term (light blue line in Figure 5a)

despite the proximity to the water table. At the same time, plateaus and ridges (high HAND) showed lower species rank change with drought severity (red line in Figure 5a). Similar patterns were observed for ant communities, but only when accounting for the long-term impact of droughts (Figure 5c). Over an extended period, fish in second-order streams were significantly impacted by impacts of drought periods, with higher WDI increasing temporal dissimilarity (red line in Figure 5b), while first-order streams showed less change in temporal dissimilarity (brown line in Figure 5b).

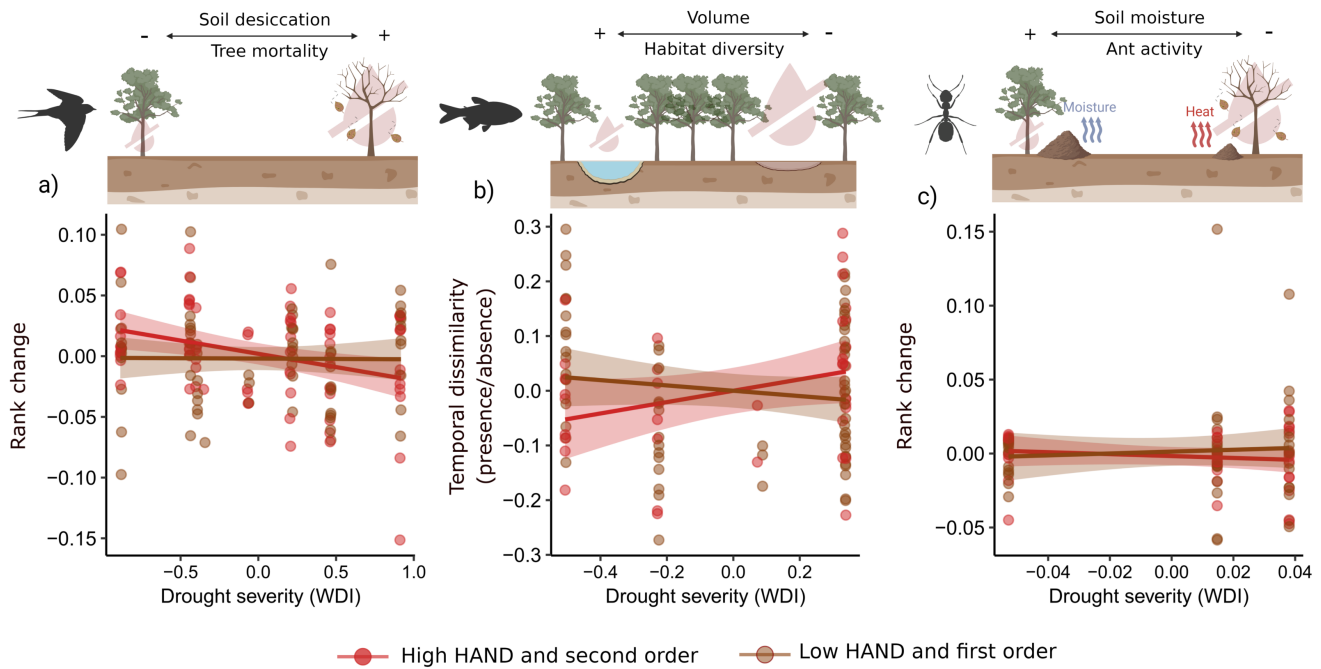


FIGURE 5 | Partial plots illustrating how local topography interacts with extreme rainfall events, affecting bird and fish compositional trends. Each panel depicts the gradient of habitat alteration in response to extreme drought (a–c) or wetness severity (d). (a, c) Bird (short-term comparison) and ant communities (long-term comparison) in upper topographic positions (high HAND) showed a decrease in species rank change as drought severity increased (brown line), while communities in lower regions (low HAND) exhibited no significant rank changes (brown line). (b) Fish from second-order streams (red lines) exhibited higher temporal dissimilarity (based on abundance and presence/absence), whereas first-order stream communities (brown lines) did not respond to the long-term effect of drought severity. Data were split into two groups based on the median HAND values for clearer representation. Lines represent the overall tendency, with shading denoting 95% confidence intervals.

4 | Discussion

The continuous monitoring of an Amazon Forest region covering periods of extreme climatic events, including droughts and wet periods, revealed varied impacts on different taxa. Animal species experienced pronounced abundance fluctuations, whereas plant species displayed relative temporal stability. Surprisingly, our findings did not support the hypothesis that local topography leads to greater temporal stability in local communities. In contrast, when intense rainfall occurred before droughts, we observed decreased temporal changes in local biodiversity over long-term comparisons, suggesting that the ‘insurance effect’ helps to maintain temporal stability within the communities over extended periods (i.e., long-term comparisons).

4.1 | Animal Communities Respond Faster Than Plants to Climate Change

As expected, we observed high abundance changes in animal species, both across samplings and between initial and final sampling, contrasting with the relative stability observed in plant species (Figure 2). These differences are likely influenced by life history traits such as longevity and survivorship. For instance, long-lived palm species may exhibit a lagged response to climate change (Compagnoni et al. 2021), as exemplified by the low abundance change in the most abundant palm species (e.g., *Oenocarpus bataua* and *Iriartella setigera*; Figure 2; Table S6). Conversely, the ant-following birds

Pithys albifrons and *Gymnopithys rufigula* declined by up to 80% throughout the survey period, while the generalist ant *Crematogaster tenuicula* increased by 75% (Figure 2; Tables S3 and S5). Beyond stochastic abundance fluctuation—where species with near-equivalent positions can swap places in rank plots—often presumed as the primary driver of temporal population changes in tropical regions (Khattar et al. 2021), our results support a primary influence of environmental filtering. This influence is evident in the striking abundance shifts of dominant species across samplings and between initial and final samplings (Figure 2), a pattern aligning with the ‘winners and losers’ paradigm attributed to species filtering due to climate change (Prugh et al. 2018). In the RFD’s streams, the alarming decline of the dominant predatory red wolf fish in just two decades (*Erythrinus erythrinus*; up to 95%; Table S4) implies a potential influence on top-down control within these ecosystems (Espírito-Santo, Rodríguez, and Zuanon 2013). If persistent, such deterministic species sorting, especially on dominant species, could lead to a marked biodiversity reconfiguration, potentially disrupting trophic interactions (Winfree et al. 2015).

The alarming decline of certain species, such as ant-following birds, could be linked to habitat fragmentation, contributing to rising extinction rates in Amazonia (Ferraz et al. 2007; Hawes et al. 2008). However, the RFD is still connected to continuous forest on its northeastern side and does not show any obvious impacts of urbanization within its limits, even though the urban sprawl of the city of Manaus has reached its southwestern limits (Figure S10). Additionally, it is estimated that the edge effects

in Central Amazonia are estimated to extend to about 300 m into the forest (Laurance et al. 2011), while RFD's permanent plots are at least 1 km distant from all borders. Therefore, the monitored communities reflect interior forest conditions, minimizing the influence of fragmentation. A similar result of marked abundance decline for ground-foraging birds was also recently reported in apparently undisturbed forests north of RFD (Stouffer et al. 2021). Thus, given the reserve's ecological integrity and limited extension of disturbances beyond borders, the observed changes are more likely driven by factors other than fragmentation.

The Amazon is experiencing an unprecedented intensification of hydrological cycles (Gloor et al. 2013), negatively affecting vegetation structure and ecosystem functioning (Esteban et al. 2021; Garcia et al. 2023). While these changes impact palm communities, they cause more pronounced temporal changes in animal communities. Despite rising mean annual rainfall in the RFD (Figure S1), the greatest changes in animal communities occurred during severe droughts (Figures S6–S8). Ant communities experienced a 36% decline in species richness and decreased temporal dissimilarity during droughts (short-term comparisons). However, these changes did not persist in the long term, which aligns with evidence that some insects respond quickly to short-term climate impacts but recover later (McCain and Garfinkel 2021). Similarly, droughts made fish communities more similar, with species gains of up to 26%. During the rainy season, lateral ponds in *terra firme* streams serve as shelters for fish species (Espírito-Santo and Zuanon 2017). When these ponds dry up during droughts, fish are forced to recolonize streams, likely explaining the increase in species richness (Borba et al. 2021). This short-term response to droughts has long-lasting effects, as observed in the long-term impacts on fish community dynamics. Unlike ants and fish, droughts increased temporal dissimilarity in bird communities, suggesting movements to more favorable microclimates, such as downslope areas (Jirinec et al. 2021). However, significant changes in community components only emerged over longer periods, with droughts reducing species richness and wet periods increasing it by up to 25%. This delayed bird response likely relates to declining resources and fewer nesting sites after repeated extreme events (Selwood et al. 2015). Palm communities, on the other hand, primarily respond to long-term climate impacts. Droughts led to decreased temporal dissimilarity and rank change, with the most pronounced effects on plateaus and ridges, likely due to their distance from groundwater sources (Rennó et al. 2008).

Overall, climate extremes produce varied and complex responses in animal and plant communities, with each taxon exhibiting unique trends. Ants respond more rapidly to short-term changes, while both birds and fish are also affected by these immediate changes, but the impacts on their communities tend to persist over extended periods. In contrast, palms display more gradual shifts, primarily responding to long-term climate impacts. This highlights the diverse ways different taxa cope with ongoing climate change in the Amazon.

4.2 | Extreme Wet Periods Buffer Drought Impact in Aquatic and Terrestrial Environments

We hypothesized that preceding extreme wet periods would mitigate the impact of subsequent droughts on local biodiversity

(the 'insurance effect' hypothesis). This sequence relies on groundwater dynamics, a pivotal factor in Amazonia's seasonal cycle. Groundwater accumulates during wet periods, slowly releasing it to maintain soil moisture and water bodies during dry spells (Miguez-Macho and Fan 2012a; Tomasella et al. 2008). Also, it directly preserves stream flow, potentially influencing fish species distribution and abundance during subsequent droughts. This hydrological memory increased long-term temporal stability comparisons in animal and plant communities by fostering favorable conditions for species persistence during drought periods.

Extreme rainfall recharges the groundwater, allowing plant species to access water resources over prolonged periods (Esteban et al. 2021). This is especially critical for palm species, which have shallow root systems that can lose access to water during soil desiccation. Accordingly, we observed reduced temporal changes in palm communities when wet periods preceded droughts. This vegetation stability can indirectly benefit other groups by sustaining buffered microclimates in the understory (Menger et al. 2024; Roberts et al. 2019). However, while palms exhibit greater temporal stability, we did not observe a similar effect on bird communities. This paradoxical trend may be due to the short-term impacts of extreme rainfall preceding droughts, which disrupt typical recovery patterns. Heavy rainfall may wash away or limit the activity of insects, a primary food source for many bird species, leading to reduced energy intake and affecting both survival and reproductive success (Öberg et al. 2015). Therefore, the buffering effect of wet periods may not sufficiently alleviate the impact of subsequent droughts, leading to greater community reordering. This disruption suggests a slower recovery trajectory for bird communities after consecutive climate disturbances, as seen in other regions (Penny, Dornelas, and Magurran 2023), where species abundance recovers slowly from successive extremes (Hillebrand and Kunze 2020).

In aquatic environments, wet periods buffer drought impacts, although the pattern is more complex. In short-term comparisons, we observed increased temporal dissimilarity in fish communities during 'wet then drought' periods. In Central Amazonian streams, heavy rainfall events raise the water table and create marginal ponds (Pazin et al. 2006), which act as refugia for fish species. These species, equipped with strategies to handle storm disturbances, later recolonize the main channel during droughts (d'Araújo Couto et al. 2018; Espírito-Santo and Zuanon 2017). Thus, the 'insurance effect' in fish communities likely results from these unique hydrological dynamics of the *terra firme* region, where topographic variation and clay soils allow for water storage and slow release (Miguez-Macho and Fan 2012a; Tomasella et al. 2008).

The buffering effect of wet periods on subsequent droughts in a central Amazonian forest highlights the importance of considering preceding extreme wet periods when evaluating drought impacts. Given that around 90% of rainfall is absorbed into the soil and recharges groundwater in Amazonia (Miguez-Macho and Fan 2012a), hydrological memory may be more common than previously assumed. This has significant implications for predicting the effects of current and future climate conditions on local biodiversity. Over extended periods, groundwater

memory can play a critical role in mitigating the severity of extreme droughts, allowing Amazonian forests to be partially 'rescued' from the harshest dry conditions when droughts are preceded by periods of intense rainfall.

4.3 | Local Topography Did Not Provide Refugia Against Climate-Driven Compositional Change

Our study also explored the expectation that environments with lower susceptibilities to extreme rainfall events could provide temporary habitat refuges, allowing organisms to retreat during adverse conditions (Costa et al. 2022; McLaughlin et al. 2017). However, our results challenged this 'environmental refugia' hypothesis across all taxa. While Selwood et al. (2015) observed fewer bird species decline during Australia's 'Big Dry' (1997–2010) in floodplain areas compared to non-floodplain zones (19.4% vs. 28.5%), their results were derived from comparing two broad areas without delving into the topographical variations within each, a gap our study aimed to address.

Contrary to our predictions, extreme droughts decreased species rank changes within bird and ant communities in the naturally drier plateau and ridge areas, unlike valleys characterized by shallow water tables. The valley landscape is much more dynamic than that of the plateaus, continuously rearranging according to episodes of droughts or wet periods. On the other hand, plateaus seem to be more stable over time, allowing for a more stable bird community. Similarly, Esteban et al. (2021) observed a decreased mortality and increased growth of the 30 most abundant tree species in the RFD in a 'wet then drought' sequence in valleys. This suggests that temporal shifts in vegetation demography might predict temporal dynamics in community reordering for other co-occurring communities. Likewise, our hypothesis posited that second-order streams, characterized by their larger size with considerable depth, slow currents, and accumulation of sand and litter banks (Walker 1995), would buffer the impact of rainfall extremes on fish temporal dynamics compared to shallow and high-sinuosity first-order streams. Yet, contrary to this prediction, we observed that droughts increased temporal fish dissimilarity in second-order streams.

Approximately 50% of the Amazonian forests cover shallow water-table (WT < 5 m deep) areas, with about 5% over deep (> 20 m) water-table regions (e.g., low HAND; Fan, Li, and Miguez-Macho 2013). If local hydro-topographic conditions buffered extreme rainfall impacts, we could expect considerable Amazonian biodiversity resilience to droughts due to prevalent moister areas. However, our findings on the RFD site, examining various biodiversity groups and metrics, do not support this expectation. Instead, we observed opposing responses in bird, fish, and ant communities—greater temporal dynamics in areas considered local refuges during adverse climate conditions—which may considerably impact predictive models. Often, these models overlook the interaction between climate change and local topographic features, potentially leading to unreliable forecasts. Thus, recognizing the variability of local conditions is critical for Amazonia's future projections, especially amidst increasing extreme climate events (Marengo et al. 2018). We also emphasize the need for similar analyses in a broad array of Amazonian sites, as soil and catchment hydrological behavior

varies with geomorphological features (Costa et al. 2022), preventing effective generalization from a single study site.

4.4 | Future Directions for Studying Climate–Biodiversity Relationships

Our two-decade-long monitoring highlights the complexity of understanding long-term biological responses to climate change, especially in extrapolating results across different taxa. For instance, palms do not necessarily represent how other plant groups respond to climate change, and ants may not represent other insects. Moreover, as our reports were based on empirical observational data, there are potential caveats that warrant consideration in future research. First, the non-synchronized sampling across taxa limits our ability to fully compare and understand the indirect effects of climate change. For example, synchronized sampling could clarify the relationship between the parallel declines of ant-following birds and army ants (e.g., *Eciton burchellii*). Future research efforts should aim for coordinated and more frequent sampling periods to facilitate direct analysis of climate variations on community metrics.

Second, our findings challenge the assumption that environmental refugia and the 'insurance effect' necessarily enhance temporal stability in biological communities in the short term, highlighting that models based solely on extreme rainfall events and topography may be insufficient. An alternative explanation could lie in species-specific sensitivities to climate change; what is 'less stressful' for one species may be stressful for another (Rosado, Roland, and Moraes 2023). The diversity of responses relates to the variety of functional traits (De Bello et al. 2021), offering a deeper understanding of local trends in climate-biodiversity studies (Evans et al. 2022). However, knowledge of traits responsive to climate change, especially in tropical regions and among animals, remains limited (Raunkiaeran shortfall; Hortal et al. 2015). Efforts to develop and collect sensitive traits (e.g., drought tolerance, thermal tolerance) combined with demographic monitoring are needed to characterize species' responses to climate change (e.g., Garcia et al. 2023; Pacifici et al. 2017).

5 | Conclusions

The biological communities we studied are experiencing changes as climate conditions intensify. While there are notable shifts in diversity, we did not observe consistent species declines over the two decades of monitoring. This suggests that the species studied have not yet reached the thresholds of their ecological niches (Colwell et al. 2008), which is an encouraging sign. Moreover, our results indicate that interactions between hydrological intensification and extreme events (droughts and extreme wet periods) are the primary source of long-term diversity change, indicating that community responses to ongoing climate change are interconnected rather than isolated for animal and plant local communities. However, further exploration of uncharted mechanisms might lead to more generalizable findings. These factors include monitoring population demography (e.g., Esteban et al. 2021) and examining species-specific response traits to climate change (Garcia et al. 2023). Furthermore, it is fundamental to persist in monitoring these

communities to understand the long-term impact of climate change on tropical biodiversity. Sustained efforts are crucial for unraveling the intricate dynamics of ecological responses to an ever-changing climate.

Author Contributions

Carlos A. S. Rodrigues-Filho: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing – original draft. **Flávia R. C. Costa:** conceptualization, data curation, investigation, methodology, project administration, supervision, visualization, writing – original draft. **Juliana Schietti:** conceptualization, writing – original draft. **Anselmo Nogueira:** conceptualization, writing – original draft. **Rafael Pereira Leitão:** conceptualization, writing – original draft. **Juliana Menger:** conceptualization, writing – original draft. **Gabriel Borba:** conceptualization, writing – original draft. **Caian Souza Gerolamo:** conceptualization, writing – original draft. **Stefano S. Avilla:** conceptualization, writing – review and editing. **Thaise Emilio:** conceptualization, writing – original draft. **Carolina Volkmer de Castilho:** conceptualization, writing – original draft. **Douglas Aviz Bastos:** conceptualization, writing – original draft. **Elisangela Xavier Rocha:** conceptualization, writing – original draft. **Itanna O. Fernandes:** conceptualization, writing – original draft. **Cintia Cornelius:** conceptualization, resources, writing – original draft. **Jansen Zuanon:** conceptualization, data curation, investigation, methodology, project administration, writing – original draft. **Jorge L. P. Souza:** conceptualization, writing – original draft. **Ana C. S. Utta:** conceptualization, writing – original draft. **Fabricio B. Baccaro:** conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, supervision, visualization, writing – original draft.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used for this article are archived at figshare.com (DOI: [10.6084/m9.figshare.25021103](https://doi.org/10.6084/m9.figshare.25021103)).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.