

Effects of water surplus over a secondary forest remain after 16 years in the Amazonia

Julia Isabella de Matos Rodrigues ⁽¹⁾, Walmer Bruno Rocha Martins ⁽¹⁻²⁾, Victor Pereira de Oliveira ⁽³⁾, Hiago Felipe Cardoso Pacheco ⁽¹⁾, José Rozendo de Lima Silva ⁽⁴⁾, Francisco de Assis Oliveira ⁽¹⁻⁴⁾, Gustavo Schwartz ⁽¹⁻⁵⁾

Water and Nutrient Manipulation in a Secondary Forest (MANFLORA) was conducted in the eastern Amazon region over eight years. In this experiment, three treatments were established: Control (CTL), Litter Removal (REM), and Soil Irrigation (IRR) within the secondary forest. The objective was to understand the effects of resource management on forest dynamics after slash-andburn agriculture. The floristic composition and vegetation structure were evaluated 16 years after the experiment's conclusion. The absolute number of species and individuals varied among CTL, IRR, and REM. Hierarchical clustering based on the Jaccard's index revealed similarity in floristic composition between CTL and IRR, both for individuals ≥ 15 cm in circumference at breast height and those in natural regeneration. Nutrient shortage through litter removal and periodic irrigation did not significantly affect the vegetation structure, likely due to the greater adaptability of species to soil and climate changes. Regarding floristic composition, REM presented long-term losses, indicating that soil nutrient availability can be a critical factor for the recovery of floristic composition in secondary forests.

Keywords: Forest Succession, Resource Management, Structural Indicators, Composition Indicators

Introduction

Restoring degraded ecosystems, which involves strategies and techniques to reverse the damage caused by environmental degradation, has become a global necessity due to the crises threatening the integrity of life on Earth (Fabbrizzi et al. 2023). Climate change, biodiversity loss and the decline of water reservoirs are current scientific concerns, resulting from the expansion of human activities such as agriculture and livestock, driven by the increasing demand for food (Bustamante et al. 2019).

In the Amazon, shifting agriculture has been the primary activity responsible for replacing natural forests with small-scale farming areas for centuries. Although considered a low-impact environmental activity due to its small scale, the increasingly shorter fallow periods are reducing the regeneration potential of ecosystems affected by shifting agriculture (Denich et al. 2005). On the other hand, maintaining forests adjacent to cultivated areas, combined with the resilience of Amazonian ecosystems, often allows positive trajectories of secondary vegetation restoration through natural regeneration (Chazdon 2017).

Natural regeneration enables the recovery of ecosystem structure (biomass, basal area, and height) and composition (species richness and diversity), which implies a gradual recovery of the ecosystem functional characteristics, such as soil moisture and fertility (Chazdon & Guariguata 2016).

These characteristics are effective indicators of ecosystem restoration, as they reflect ecosystem conditions, particularly regarding abiotic variations like climate events and changes in the physical and chemical properties of soil (Barbosa et al. 2021). On the other hand, secondary forests are typically characterized by substantial increases in height and diameter of trees in the early stages of succession, ensuring a high potential for carbon sequestration from the atmosphere (Nunes et al. 2020). In this context, understanding the factors underlying the development of secondary forests is essential for achieving global restoration goals, including Brazil's commitment to restore 12 million hectares by 2030 (PLANAVEG 2017).

Resource availability, especially water and nutrients, is one of the key factors influencing plant development in forest ecosystems (Rocha et al. 2023). This is particularly significant in the Amazon due to the high soil acidity and intense weathering, which result in low natural soil fertility and a high dependence on nutrient cycling for ecosystem maintenance (Hoosbeek et al. 2021). The decomposition of litter, i.e., the layer of forest residues deposited on the ground, stands out as the primary source of nutrition for the soil-plant system (Elias et al. 2019). The availability of elements like Ca and K in the soil are positively correlated with the decomposition rate (Piza et al. 2021), and nutrient return depends on the litter flux throughout the year (Zhu et

Frequent and intense rains, which are

@ Julia Isabella de Matos Rodrigues (juliaisabellarodrigues@gmail.com)

Received: Dec 05, 2023 - Accepted: Apr 03, 2025

Citation: Rodrigues JIDM, Martins WBR, Oliveira VPD, Pacheco HFC, Silva JRDL, Oliveira FDA, Schwartz G (2025). Effects of water surplus over a secondary forest remain after 16 years in the Amazonia. iForest 18: 234-241. - doi: 10.3832/ifor4537-018 [online 2025-09-06]

Communicated by: Paola Mairota

^{□ (1)} Graduate Program in Forestry Science, Av. Presidente Tancredo Neves, 2501, Belém, Pará, 66077-530 (Brazil); (2) Federal Rural University of Amazonia, Tv. Pau Amarelo, Capitão Poço, Pará, 68650-000 (Brazil); (3) National Institute of Amazonia Research, Av. Constelação Cruzeiro do Sul, Manaus, Amazonas, 69060-062 (Brazil); (4) Federal Rural University of Amazonia, Department of Agrarian Science, Av. Presidente Tancredo Neves, 2501, Belém, Pará, 66077-530 (Brazil); (5) Embrapa Eastern Amazonia, Tv. Dr. Enéas Pinheiro, Belém, Pará, 66095-903 (Brazil)

common in much of the Amazon, promote the activity of soil entomofauna and microorganisms that directly contribute to litter decomposition (Reyes et al. 2019). They are also responsible for the plant's eco-physiological responses during its development, including radial stem expansion (Kaewmano et al. 2022). For this reason, changes in weather patterns can result in significant disruptions to vegetation composition and forest dynamics, leading to losses in carbon storage.

The Water and Nutrient Manipulation in a Successional Forest project in the Eastern Amazonia (MANFLORA) was developed to understand the long-term effects of resource management on the dynamics of a secondary forest (Vasconcelos et al. 2007, 2008, 2012). In the MANFLORA's experimental plots, the effects of nutrient reduction through the complete removal of all stored litter and periodic irrigation during drier periods were tested over eight years. The following question was addressed: Are there long-term effects on the floristic composition and structure of secondary forests in response to resource manipulation? This study hypothesizes that longterm irrigation and nutrient reduction would alter the floristic composition and structure of the secondary forest.

Materials and Methods

Study area

The study was conducted in the experimental plots of MANFLORA (o1° 19′ 16″ S, 47° 57′ 50″ W), located at the Castanhal School Farm (Fazenda Escola de Castanhal - FEC), which belongs to the Federal Rural University of the Amazonia, in the municipality of Castanhal, Pará state, Eastern Amazonia, Brazil (Fig. 1). According to Köppen's classification, the climate of the study area is Af3, with an average annual

rainfall of 2000-2500 mm (Alvares et al. 2013). The wettest period occurs from December to May, while the drier season spans from June to November (Rangel-Vasconcelos et al. 2005). The topography is gently undulating, and the soils are identified as Yellow Ferrosols, characterized by low natural fertility (Tenório et al. 1999). The original vegetation was classified as Dense Ombrophilous Forest; however, it is now predominantly composed of secondary forests (IBGE 2012).

MANFLORA began in 1999 in a forest that had undergone 12 years of natural regeneration after the cessation of agricultural activity. It consisted of control plots (CTL) without human intervention and two resource management treatments: Soil Irrigation (IRR) and Litter Removal (REM). Four permanent plots, each measuring 400 m^2 (20 × 20 m), were established for each treatment, with a minimum distance of 10 m among them. In the IRR treatment, 5 mm of water was supplied per day for 30 minutes during the lower precipitation months (July to November) using microperforated tapes. In the REM treatment, the litter deposited on the ground was removed entirely every two weeks through plastic rakes. The experiment was concluded in mid-2007, with the secondary forest at 20 years of age. In 2023, sixteen years after the experiment's conclusion, an evaluation was carried out on ecological indicators related to the composition and structure of the vegetation.

Experiment design and data collection

The experimental design and spatial distribution of the permanent plots used in MANFLORA is displayed in Fig. 1 (Vasconcelos et al. 2007, 2008). In these plots, we assessed floristic composition, both the horizontal and vertical forest structure, and estimated above-ground biomass (AGB).

Floristic composition and biomass estimation

A floristic inventory of all arboreal and shrub individuals with a Circumference at Breast Height (CBH) ≥ 15 cm was conducted within a 10 × 10 m area established within each 400 m² plot (20 × 20 m). For these individuals, the total height (Ht) was also estimated. Additionally, a 2 × 2 m area was randomly placed within each subplot to assess natural regeneration (NR). Here, the Ht and CCH (Circumference at Collar Height) of all arboreal individuals with Ht ≥ 10 cm and CBH < 15 cm were measured, using rulers and calipers. When in situ identification was not possible, samples were collected and subsequently identified by comparing them with specimens from the IAN Herbarium of Embrapa Eastern Amazonia, in Belém, Pará, Brazil. Species were classified into ecological groups as pioneer, early secondary, late secondary, and climax, following the classification proposed by Gandolfi et al. (1995). The conservation status of each species was classified as "Critically Endangered" (CR), "Vulnerable" (VU), or "Least Concern" (LC), according to the International Union for Conservation of Nature (IUCN 2020).

Above-ground biomass (AGB) was estimated using the allometric equation (eqn. 1) proposed by Chave et al. (2014), with wood density data for each species from the Global Wood Density Database (Chave et al. 2009) for the Neotropical region. Total AGB (in kg) was the sum of AGB for all individuals in each treatment, which was subsequently converted into megagrams per hectare (Mg ha 1):

$$AGB = 0.0673 \cdot (\rho D^2 H)^{0.976}$$
 (1)

where ρ is the wood density (g cm³), D is the tree diameter (cm), and H is the tree height (m).

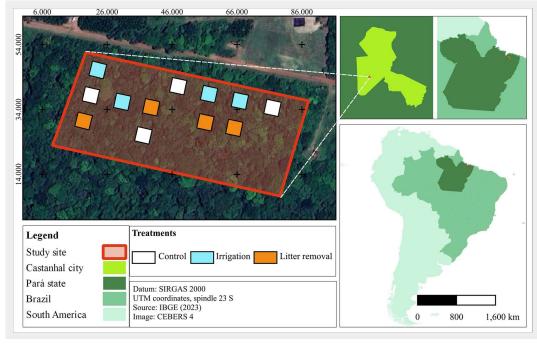


Fig. 1 - Fragment of secondary forest 16 years after the conclusion of the Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MAN-FLORA). Squares represent the plots assigned to Control (CTL), Irrigation (IRR), and Nutrient Removal (REM) treatments.

Measures of alpha diversity

Alpha diversity indices were assessed using the Shannon index (Magurran 1958), Margalef index (Margalef 1958), Pielou's evenness, and Simpson index (Brower et al. 1998).

Horizontal and vertical structure

The Importance Value Index (IVI) was calculated by summing the means of Relative Dominance (RDom), Relative Frequency (RFreq), and Relative Density (RDens) values, following the methodology proposed by Müeller-Dombois & Ellenberg (1974). The Expanded Importance Value Index (EIVI) was calculated by summing the means of RDom, RFreq, RDens, Relative Sociological Position (PSR), and Relative Natural Regeneration (RNR) values, as per Finol (1971).

Data analysis

Species and individual density data, as well as the estimated biomass, were checked for normality and homoscedasticity using the Shapiro-Wilk and Levene tests, respectively, both at a 5% significance level. Once these assumptions were met, analysis of variance (ANOVA, p < 0.05) was con-

ducted. In cases of significant differences, averages between treatments were compared using the Tukey test (p < 0.05) for hypothesis testing. The similarity of species richness between treatments was evaluated through rarefaction curves for individuals. Sampling effort was standardized by the number of individuals in the sampled area (Gotelli & Colwell 2001), with the assistance of the "iNEXT" package in R software v. 4.2.0 (Chao et al. 2014, Hsieh et al. 2016, R Development Core Team 2023). To assess floristic-structural dissimilarity, a binary matrix of species presence (1) and absence (o) was used to calculate the Jaccard's index. Subsequently, hierarchical clustering was performed and visualized in a heatmap. Species richness data were analyzed using a Generalized Linear Model (GLM) with a Poisson link function, considering the treatment and ecological groups as factors.

Results

Floristic composition and biomass estimation

Using a threshold of CBH ≥ 15 cm, we recorded a total of 114 individuals of 32

species and 19 families in CTL, 85 individuals of 22 species and 15 families in REM, and 110 individuals of 29 species and 17 families in IRR, respectively. Regarding natural regeneration (NR), there were 108, 105, and 81 individuals of 11, 12, and 13 species in CTL, IRR, and REM, distributed in 9, 11, and 9 families in the same order.

Considering individuals with CBH ≥ 15 cm, nine species were found to be common across all treatments. Specifically, the CTL and IRR treatments each presented nine exclusive species, while REM had four unique species (Fig. 2A). In natural regeneration, three species (Acosmium lentiscifolium, Cecropia pachystachya, and Ocotea guianensis) occurred in all treatments. Additionally, two species were exclusive to CTL, five were exclusive to IRR, and six were exclusive to REM (Fig. 3A). The hierarchical clustering based on the Jaccard's index indicated similarity in floristic composition between CTL and IRR, with greater distance between IRR and REM in both samples (Fig. 3b and Fig. 4b). However, AGB did not differ between treatments ($F_{[2:0]}$ = 1.296; p = 0.320), with averages of 64.16 ± 49.68 Mg ha⁻¹, 77.36 ± 31.33 Mg ha⁻¹, and 118.02 ± 62.01 Mg ha⁻¹ for CTL, IRR, and

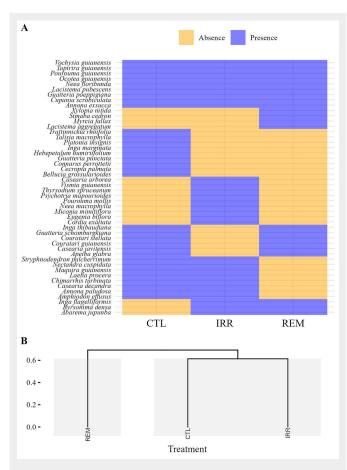


Fig. 2 - Heatmap based on presence and absence of species (A) and dendrogram cluster with Jaccard dissimilarity (B), considering only individuals ≥ 15 cm in CBH, 16 years after Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). Control (CTL), Irrigation (IRR), Nutrient Removal (REM).

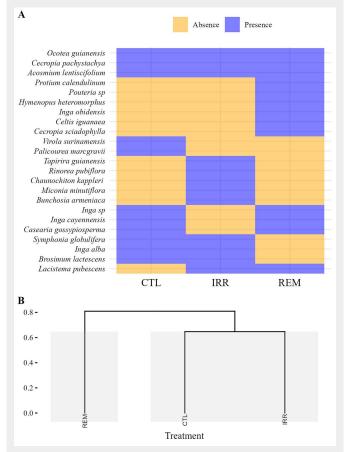


Fig. 3 - Heatmap based on presence and absence of species (A) and dendrogram cluster with Jaccard dissimilarity (B), considering only individuals from natural regeneration, 16 years after Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). Control (CTL), Irrigation (IRR), Nutrient Removal (REM).

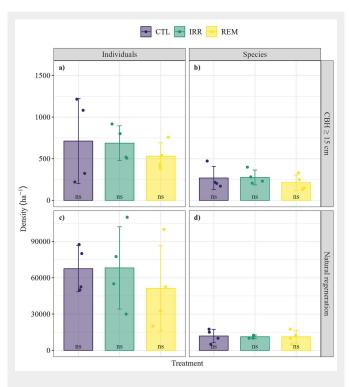


Fig. 4 - Average ± standard deviation (SD) of stand and species density of individuals with CBH ≥ 15 cm (a, b) and NR (c, d) in a fragment of successional forest, 16 years after Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). (CTL): Control; (IRR): Irrigation; (REM): Nutrient Removal; (ns): no significant difference between treatments for both stand and species density. Dots represent the species or individual density in sample units of the respective treatments.

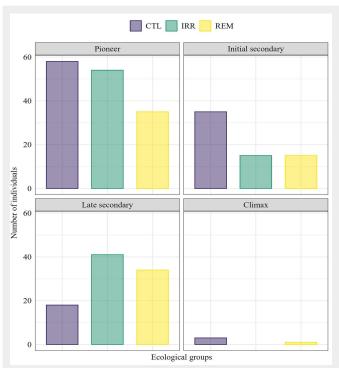


Fig. 5 - Number of individuals (CBH \geq 15 cm) for each ecological group in 400 m² of a successional forest fragment, 16 years after Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). (CTL): Control; (IRR): Irrigation; (REM): Nutrient Removal.

REM, respectively.

Stand density ranged from 531.25 \pm 159.92 (standard deviation, SD) to 712.50 \pm 510.51

individuals per hectare in REM and CTL, respectively (Fig. 4a), while for species, density ranged from 212.50 ± 92.42 to $275.00 \pm$

Tab. 1- Generalized Linear Model (GLM) of Poisson explaining species richness of ecological groups in a successional forest fragment, 16 years after Water and Nutrient Manipulation in a Successional Forest project in the Eastern Amazonia project (MAN-FLORA). The predictor attributes were richness, treatments, and ecological groups. (IRR): Irrigation; (REM): Nutrient Removal.

| Coefficients | Estimate | Std. Error | z value | Pr (> z) |
|--------------------------------------|----------|------------|---------|-----------|
| (Intercept) | -0.519 | 0.975 | -0.533 | 0.594 |
| [Treatment] IRR | -0.056 | 0.431 | -0.131 | 0.896 |
| [Treatment] REM | -0.167 | 0.434 | -0.385 | 0.701 |
| [Ecological group] Pioneers | 1.938 | 1.007 | 1.925 | 0.054 |
| [Ecological group] Initial secondary | 1.687 | 1.019 | 1.655 | 0.098 |
| [Ecological group] Late secondary | 1.808 | 1.013 | 1.785 | 0.074 |

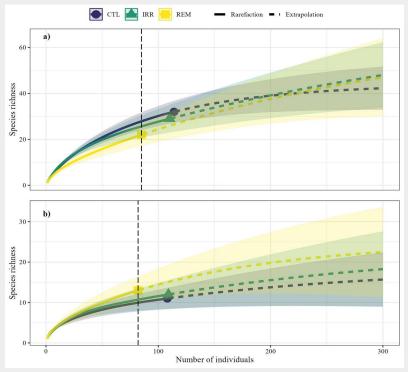
Tab. 2 - Alpha diversity measures for species with individuals ≥ 15 cm in CBH and natural regeneration in a successional forest fragment, 16 years after Water and Nutrient Manipulation in a Successional Forest project in the Eastern Amazonia project (MAN-FLORA). (CTL): Control; (IRR): Irrigation; (REM): Litter removal.

| Treatment | Margalef | Simpson | Shannon | Pielou |
|-----------|----------|---------|---------|--------|
| CTL | 0.18 | 0.89 | 2.84 | 0.76 |
| IRR | 0.16 | 0.87 | 2.73 | 0.76 |
| REM | 0.19 | 0.86 | 2.52 | 0.73 |

88.98 species per hectare for REM and IRR, respectively (Fig. 4b). However, in both cases, no significant differences were observed between treatments (p > 0.05 - Fig.4). In terms of NR, there were no statistically significant differences either, with species density ranging from 11,250 \pm 1,443 to 11,875 \pm 5,443 species per hectare for IRR and CTL, respectively (Fig. 4c), and stand density ranging from 51,250 \pm 35,148 to 68,125 \pm 33,966 individuals per hectare for REM and IRR, in that order (Fig. 4d).

Pioneer species were predominant in CTL and IRR (Fig. 5). In the group of initial secondary species, most individuals (53.85%) corresponded to CTL. In contrast, IRR (44.09%) and REM (36.56%) had the highest proportion of individuals belonging to late secondary species (Fig. 5). However, regarding species richness, the GLM results did not indicate significant differences among ecological groups and treatments (Tab. 1). Regarding the conservation status of species, only a species classified as "VU" (Vulnerable) was found in REM and CTL, namely, Couratari guianensis Aubl. with one individual in each treatment. Two species (Platonia insignis Mart. and Couratari stellata A. C. Sm.) had no data registered in the IUCN Red List, and the remaining species found were classified as "LC" (Least Concern).

Fig. 6 - Rarefaction curves based on samples in a secondary forest fragment, 16 years after Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). Considering only individuals ≥ 15 cm in CBH cm (a) and individuals from the natural regeneration (b). Solid lines represent the average of species richness observed, while dashed lines are the estimated species richness. The vertical line parallel to the y-axis corresponds to the rarefied species richness, calculated based on the number of individuals from the ecosystem with the lowest abundance. Shaded areas represent 95% confidence intervals. Control (CTL), Irrigation (IRR), Nutrient Removal (REM).



Tab. 3 - Top ten species with the highest Importance Value Index (IVI) and Expanded Importance Value Index (EIVI) in a successional forest fragment, 16 years after the experiment termination: Control (CTL), Irrigation (IRR), and Litter Removal (REM) from the Water and Nutrient Manipulation in a Successional Forest in the Eastern Amazonia project (MANFLORA). (RDen): Relative Density (%); (RDom): Relative Dominance (%); (RFreq): Relative Frequency (%); (RSP): Relative Sociological Position (%); (RNR): Relative Natural Regeneration (%).

| eatme | nt Species | RDen | RDom | RFreq | IVI | RSP | RNR | EIVI |
|-------|---|-------|-------|-------|-------|-------|-------|-------|
| CTL | Myrcia fallax | 23.87 | 0.26 | 6.45 | 10.19 | 21.74 | 40.57 | 18.58 |
| | Cecropia pachystachya | 12.61 | 0.19 | 6.45 | 6.41 | 14.58 | 24.78 | 11.72 |
| | Lacistema pubescens | 14.86 | 14.38 | 4.84 | 11.36 | 16.25 | 0.00 | 10.0 |
| | Ocotea guianensis | 4.95 | 8.53 | 4.84 | 6.11 | 5.26 | 10.22 | 6.7 |
| | Cupania scrobiculata | 5.86 | 4.61 | 4.84 | 5.10 | 5.84 | 0.00 | 4.2 |
| | Connarus perrottetii var. angustifolius | 3.15 | 9.63 | 3.23 | 5.34 | 2.72 | 0.00 | 3.7 |
| | Annona exsucca | 3.60 | 7.83 | 3.23 | 4.89 | 2.78 | 0.00 | 3.4 |
| | Palicourea marcgravii | 2.25 | 0.33 | 3.23 | 1.94 | 2.60 | 6.07 | 2.9 |
| | Annona paludosa | 1.35 | 3.15 | 4.84 | 3.11 | 1.56 | 0.00 | 2.1 |
| | Guatteria poeppigiana | 1.35 | 5.54 | 3.23 | 3.37 | 0.17 | 0.00 | 2.0 |
| | Myrcia fallax | 31.05 | 0.07 | 5.00 | 12.04 | 23.95 | 54.03 | 22.8 |
| IRR | Pourouma guianensis | 10.50 | 8.66 | 6.67 | 8.61 | 12.56 | 0.00 | 7.6 |
| | Ocotea guianensis | 5.02 | 14.05 | 5.00 | 8.02 | 4.93 | 5.73 | 6.9 |
| | Lacistema pubescens | 6.85 | 5.34 | 6.67 | 6.29 | 7.75 | 2.26 | 5.7 |
| | Cecropia pachystachya | 5.02 | 0.46 | 5.00 | 3.49 | 6.61 | 10.02 | 5.4 |
| | Amphiodon effusus | 4.57 | 14.83 | 1.67 | 7.02 | 5.17 | 0.00 | 5.2 |
| | Tapirira guianensis | 5.48 | 3.12 | 3.33 | 3.98 | 6.37 | 6.73 | 5.0 |
| | Annona exsucca | 3.20 | 6.10 | 5.00 | 4.77 | 2.95 | 0.00 | 3.4 |
| | Guatteria poeppigiana | 2.74 | 5.83 | 5.00 | 4.52 | 1.51 | 0.00 | 3.0 |
| | Brosimum lactescens | 2.28 | 0.20 | 3.33 | 2.91 | 3.00 | 5.73 | 2.9 |
| | Myrcia fallax | 27.54 | 0.94 | 6.12 | 11.53 | 12.94 | 43.73 | 18.2 |
| | Lacistema pubescens | 17.96 | 32.20 | 8.16 | 19.44 | 10.66 | 2.71 | 14.3 |
| | Ocotea guianensis | 10.18 | 35.67 | 6.12 | 17.32 | 2.58 | 2.88 | 11.4 |
| | Cecropia pachystachya | 9.58 | 0.06 | 6.12 | 5.25 | 6.13 | 18.85 | 8.1 |
| REM | Guatteria poeppigiana | 4.79 | 4.35 | 6.12 | 5.09 | 1.94 | 0.00 | 3.4 |
| | Inga obidensis | 2.40 | 0.01 | 4.08 | 2.16 | 1.53 | 7.10 | 3.0 |
| | Cupania scrobiculata | 4.79 | 2.03 | 4.08 | 3.63 | 2.79 | 0.00 | 2.7 |
| | Casearia gossypiosperma | 3.59 | 0.13 | 2.04 | 1.92 | 2.30 | 5.63 | 2.7 |
| | Inga flagelliformis | 2.40 | 2.05 | 6.12 | 3.52 | 0.97 | 0.00 | 2.3 |
| | Tapirira guianensis | 1.20 | 3.52 | 4.08 | 2.93 | 0.20 | 0.00 | 1.80 |

Horizontal and vertical structure

In all treatments, Myrcia fallax (Rich.) DC. showed the highest relative density and natural regeneration (Tab. 3). Lacistema pubescens Mart. showed a low IVI in IRR only (Tab. 3). After M. fallax, Cecropia pachystachya Trécul contributed the most to NR in all treatments. Among the species with the highest EIVI, five (M. fallax, Ocotea guianensis Aubl., L. pubescens, Guatteria poeppigiana Mart.) were common across all treatments. Tapirira guianensis Aubl. was exclusive to the treatments with resource changes, and Annona exsucca D.C. was among the highest EIVI only for CTL and IRR (Tab. 3).

Discussion

Understanding how resource management affects the long-term floristic composition and vegetation structure is crucial in the current context, given the urgent need to maintain the dynamics of secondary forests and optimize tropical forest restoration. Our initial hypothesis that periodic irrigation and nutrient reduction alter the floristics and structure of a secondary forest was partially supported, as residual effects of the treatments were evident only in species composition. This addresses the scientific question of the study and highlights the ecosystem's structural resilience in the medium term.

Resource management and its influence on forest resilience

Although water deficit can reduce evapotranspiration rates by up to 20% in fragmented forest ecosystems (Numata et al. 2021) and is closely related to the loss of structural attributes of the ecosystem, such as above-ground biomass and soil density (Abbasi et al. 2022), our results showed that periodic irrigation and the reduction of nutrients through leaf litter removal had no residual effects on vegetation structure after 16 years. This is likely due to the greater tolerance of Amazonian tree species to edaphoclimatic changes (Garcia et al. 2021). It is worth noting that pioneer species (i.e., early colonizers) are characterized by a strategy of rapid dispersal and reproduction. They maintain dominance in the first 20 years after a disturbance and can even interrupt succession when they hyper-dominate the ecosystem (García-Quintana et al. 2020). In this study, although there were many pioneer species, a balance was achieved with species from other groups, especially late successional species, which showed a higher abundance in the treatments with resource manipula-

The time required for the complete restoration of floristic composition in tropical forests remains a significant challenge for scientific research. Factors such as topography, climate, seed availability, and dispersion interfere with the restoration of forest diversity (Rufino et al. 2023). However, the pattern revealed by the cluster dendro-

gram showed that soil nutrient availability can directly influence the long-term development of naturally regenerated individuals, probably because they require more nutrients to develop during the seedling stage. The similarity between CTL and IRR in floristic composition can be attributed to the efficient use of water by Amazonian trees (Garcia et al. 2021), as the distribution of individuals may have been influenced by soil water availability. This finding is similar to the results reported by Kupers et al. (2019), suggesting that inadequate irrigation may have compelled individual trees to optimize their water usage. This is particularly significant in tropical secondary forests, where nutrient manipulation impacts the above-ground productivity (Wright 2019).

AGB values detected in this study support the evidence that human disturbances are the primary drivers of biomass reduction in tropical secondary forests, primarily due to the regeneration of low wood density species, such as pioneer and early secondary species (Buragohain et al. 2023). In secondary forests, biomass accumulation is influenced by a wide range of environmental conditions (Suarez et al. 2023). Most species have low wood density, due to their rapid growth and little investment in radial structure (Azman et al. 2021), resulting in a lower potential for carbon storage in their tissues; for example, M. fallax had the highest EIVI in CTL, IRR, and REM. The predominance of this species may be related to its biological characteristics, including high dispersal efficiency and rapid colonization, allowing widespread regeneration in disturbed ecosystems. Furthermore, its antifungal and antibacterial properties promote the germination of its seeds (Gatto et al. 2020).

The return of biomass is gradual, even with resource management

In tropical secondary forests, structural and compositional variables are key predictors of AGB accumulation, as highlighted by Villa et al. (2020). Although compositional differences were observed, we found a similar forest structure among the treatments, indicating that the recovery of carbon stocks in ecosystems can be attributed to the rapid growth of native tree species, which leads to increased litterfall, organic carbon, and below-ground biomass (Shimamoto et al. 2018).

The findings of the present study may also be related to the high abundance of thin individuals, characterized by low biomass and carbon stock. This is a feature of ecosystems in post-shifting cultivation (Villa et al. 2019). In addition, the presence of genera like *Inga*, *Pourouma*, and *Cecropia*, among the species with the highest IVI in all treatments, indicates that the studied ecosystem is still in a successional stage, as these species are indicators of disturbed ecosystems (García-Quintana et al. 2020). Secondary forests can take up to

a century to reach a carbon stock aboveground similar to that of primary forests. In forests subject to repeated burns, the rate of carbon accumulation recovery is 75% lower than in native forests and stabilizes between 11 and 40 years (Heinrich et al. 2021). The AGB tends to decrease with disturbance intensity and increase with the canopy cover of surrounding trees (Suarez et al. 2023).

Conclusion

Carbon sequestration contributes to achieving the goals of reducing carbon emissions to the atmosphere as established in large-scale agreements such as the Bonn Challenge and the New York Declaration on Forests.

No significant effects of resource management on the structure of the secondary forest were identified 16 years after the completion of the MANFLORA experiment, highlighting the structural resilience of the ecosystem and tropical forests. However, the litter nutrient removal had long-term effects on floristic composition, suggesting that soil nutrient availability is a critical factor for floristic recovery in secondary forests.

Acknowledgment

This study was financed in part by the CAPES - Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil - Finance Code 001. CAPES granted a master scholarship for JIMR (Process 88887.716287/2022-00), HFCP (Process 88887.805686/2023-00) and doctoral scholarship for VPO (Process 88887.644953/2021-00). The Ecosystem and Watershed Management Laboratory at the Federal Rural University of Amazonia served as the basis for processing data and samples.

References

Abbasi UA, Mattsson E, Nissanka SP, Ali A (2022). Biological, structural and functional responses of tropical forests to environmental factors. Biological Conservation 276: 109792. - doi: 10.1016 /j.biocon.2022.109792

Alvares CA, Stape JL, Sentelhas PC, De Moraes Gonçalves JL, Sparovek G (2013). Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22: 711-728. - doi: 10.1127/0941-2948/2013/0507

Azman MS, Sharma S, Shaharudin MAM, Hamzah ML, Adibah SN, Zakaria RM, MacKenzie RA (2021). Stand structure, biomass and dynamics of naturally regenerated and restored mangroves in Malaysia. Forest Ecology and Management. 482: 118852. - doi: 10.1016/j.foreco.20 20.118852

Barbosa RS, Pereira GFM, Ribeiro SS, Hage ALF, Costa GF, Salomão RP, Schwartz G (2021). Key species selection for forest restoration after bauxite mining in the Eastern Amazon. Ecological Engineering 162 (1): 106190. - doi: 10.1016/j.ecoleng.2021.106190

Brower JE, Zar JH, Ende Von CN (1998). Field and laboratory methods for general ecology (4th edn). M-H Education Editions, Boston, MS,

USA, pp. 288.

Buragohain MK, Dar AA, Babu KN, Parthasarathy N (2023). Tree community structure, carbon stocks and regeneration status of disturbed lowland tropical rain forests of Assam, India. Trees, Forests and People 11: 100371. - doi: 10.1016/j.tfp.2023.100371

Bustamante MMC, Silva JS, Scariot A, Sampaio AB, Mascia DL, Garcia E, Sano E, Fernandes GW, Durigan G, Roitman I, Figueiredo I, Rodrigues RR, Pillar VD, De Oliveira AO, Malhado AC, Alencar A, Vendramini A, Padovezi A, Carrascosa H, Freitas J, Siqueira JA, Shimbo J, Generoso LG, Tabarelli M, Biderman R, De Paiva Salomão R, Valle R, Junior B, Nobre C (2019). Ecological restoration as a strategy for mitigating and adapting to climate change: lessons and challenges from Brazil. Mitigation and Adaptation Strategies for Global Change 24: 1249-1270. - doi: 10.1007/s11027-018-9837-5

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45-67. - doi: 10.1890/13-0133.1

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009). Towards a worldwide wood economics spectrum. Ecology Letters 12: 351-366. - doi: 10.1111/j.1461-0248.2009.01285.x

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC, Henry M, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20: 3177-3190. - doi: 10.1111/gcb. 12629

Chazdon RL, Guariguata MR (2016). Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48: 716-730. - doi: 10.1111/btp. 12381

Chazdon RL (2017). Landscape restoration, natural regeneration, and the forests of the future. Annals of the Missouri Botanical Garden 102: 251-257. - doi: 10.3417/2016035

Denich M, Vlek P, Deabreusa T, Vielhauer K, Lucke W (2005). A concept for the development of fire-free fallow management in the Eastern Amazon, Brazil. Agriculture, Ecosystems and Environment 110: 43-58. - doi: 10.1016/j.agee.2005.05.005

Elias F, Marimon Junior BH, Oliveira FJM, Oliveira JCA, Marimon BS (2019). Soil and topographic variation as a key factor driving the distribution of tree flora in the Amazonia/Cerrado transition. Acta Oecologica 100: 103467. - doi: 10.1016/j.actao.2019.103467

Fabbrizzi E, Giakoumi S, De Leo F, Tamburello L, Chiarore A, Colletti A, Coppola M, Munari M, Musco L, Rindi F, Rizzo L, Savinelli B, Franzitta G, Grech D, Cebrian E, Verdura J, Bianchelli S, Mangialajo L, Nasto I, Sota D, Orfanidis S, Papadopoulou NK, Danovaro R, Fraschetti S (2023). The challenge of setting restoration targets for macroalgal forests under climate changes. Journal of Environmental Manage-

ment 326: 116834. - doi: 10.1016/j.jenvman.2022.

Finol UH (1971). Nuevos parámetros a considerarse en el analisis estructural de las sevas virgenes tropicales [New parameters to be considered in the structural analysis of tropical virgin forests]. Revista Florestal Venezoelana 21: 29-42. [in Spanish]

Gandolfi S, Leitão Filho HF, Bezerra CL (1995). Levantamento florístico e caráter sucessional das espécies arbustivo-arbóreas de uma florestal mesófila semidecídua no municípío de Guarulhos, SP [Floristic survey and successional character of shrub-tree species of a semi-deciduous mesophilic forest in the municipality of Guarulhos, SP]. Revista Brasileira de Biologia 55: 753-767. [in Portuguese] [online] URL: http://www.researchgate.net/publication/2594

Garcia MN, Ferreira MJ, Ivanov V, Dos Santos VAHF, Ceron JV, Guedes AV, Saleska SR, Oliveira RS (2021). Importance of hydraulic strategy trade-offs in structuring response of canopy trees to extreme drought in central Amazon. Oecologia 197: 13-24. - doi: 10.1007/s00442-021-04924-9

García-Quintana Y, Arteaga-Crespo Y, Torres-Navarrete B, Robles-Morillo M, Bravo-Medina C, Sarmiento-Rosero A (2020). Ecological quality of a forest in a state of succession based on structural parameters: a case study in an evergreen Amazonian-Andean forest, Ecuador. Heliyon 6: e04592. - doi: 10.1016/j.heliyon.2020.e04

Gatto LJ, Fabri NT, Souza AM, Fonseca NST, Furusho AS, Miguel OG, Dias JFG, Zanin SMW, Miguel MD (2020). Chemical composition, phytotoxic potential, biological activities and antioxidant properties of *Myrcia hatschbachii* D. Legrand essential oil. Brazilian Journal of Pharmaceutical Sciences 56: e18402. - doi: 10.1590/s2175-97902019000318402

Gotelli NJ, Colwell RK (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391. - doi: 10.1046/j.1461-0248.2001.00230.x

Heinrich VHA, Dalagnol R, Cassol HLG, Rosan TM, De Almeida CT, Silva Junior CHL, Campanharo WA, House JI, Sitch S, Hales TC, Adami M, Anderson LO, Aragão LEOC (2021). Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. Nature Communications 12: 1785. - doi: 10.1038/s41467-021-22050-1

Hoosbeek M, Schaap KJ, Quesada CA (2021). Depth differentiation of carbon, nitrogen and phosphorous cycling in litter and soil in Central Amazonia: availability of organic P may limit the response to increasing atmospheric CO₂. SSRN Electronic Journal 107 (20): 5. - doi: 10.2139/ssrn.3990652

Hsieh TC, Ma KH, Chao A (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7: 1451-1456. - doi: 10.1111/2041-210X.12613

IBGE (2012). Manual técnico da vegetação brasileira [Technical manual of Brazilian vegetation] (2nd edn). Instituto Brasileiro de Geografia e Estatística - IBGE, Rio de Janeiro, Brazil, pp. 271. [in Portuguese]

IUCN (2020). IUCN red list of threatened species. International Union for Conservation of Nature - IUCN, website. [online] URL: http://www.iucn.org/resources/conservation-tools/iucn-red-list-threatened-species

Kaewmano A, Fu P-L, Fan Z-X, Pumijumnong N, Zuidema PA, Bräuning A (2022). Climatic influences on intra-annual stem radial variations and xylem formation of *Toona ciliata* at two Asian tropical forest sites with contrasting soil water availability. Agricultural and Forest Meteorology 318: 108906. - doi: 10.1016/j.agrformet. 2022.108906

Kupers SJ, Engelbrecht BMJ, Hernández A, Wright SJ, Wirth C, Rüger N (2019). Growth responses to soil water potential indirectly shape local species distributions of tropical forest seedlings. Journal of Ecology 107: 860-874. doi: 10.1111/1365-2745.13096

Magurran AE (1958). Ecological diversity and its measurement. Springer, Dordrecht, Netherlands, pp. 180. - doi: 10.1007/978-94-015-7358-0 Margalef R (1958). Information theory in ecology. General Systems 3: 36-71.

Müeller-Dombois D, Ellenberg H (1974). Aims and methods of vegetation ecology. John Wiley and Sons, New York, USA, pp. 23. [online] URL: http://www.geobotany.org/library/pubs/Mueller-Dombois1974_AimsMethodsVegEcol_ch5.pdf

Numata I, Khand K, Kjaersgaard J, Cochrane MA, Silva SS (2021). Forest evapotranspiration dynamics over a fragmented forest landscape under drought in southwestern Amazonia. Agricultural and Forest Meteorology 306: 108446. doi: 10.1016/j.agrformet.2021.108446

Nunes S, Gastauer M, Cavalcante RBL, Ramos SJ, Caldeira CF, Silva D, Rodrigues RR, Salomão R, Oliveira M, Souza-Filho PWM, Siqueira JO (2020). Challenges and opportunities for large-scale reforestation in the Eastern Amazon using native species. Forest Ecology and Management 466: 118120. - doi: 10.1016/j.foreco.2020. 118120

Piza PA, Suárez JC, Andrade HJ (2021). Litter decomposition and nutrient release in different land use located in Valle del Cauca (Colombia). Agroforestry Systems 95: 257-267. - doi: 10.1007/s10457-020-00583-6

PLANAVEG (2017). Plano Nacional de Recuperação da Vegetação Nativa [National Plan for the Recovery of Native Vegetation]. MMA, Brasília, Brazil, pp. 73. [in Portuguese]

R Development Core Team (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. [online] URL: http://www.r-project.org Rangel-Vasconcelos LGT, Zarin DJ, Carvalho CJR, Santos MMLS, Vasconcelos SS, Oliveira FA (2005). Carbono, nitrogênio e atividade da biomassa microbiana de um solo sob vegetação secundária de diferentes idades na Amazônia oriental [Carbon, nitrogen, and microbial biomass activity of the soil under secondary vegetation of different ages in eastern Amazonia]. Revista de Ciências Agrárias 44: 49-63. [in Portuguese]

Reyes HA, Ferreira PFA, Silva LC, Da Costa MG, Nobre CP, Gehring C (2019). Arbuscular mycorrhizal fungi along secondary forest succession

at the eastern periphery of Amazonia: seasonal variability and impacts of soil fertility. Applied Soil Ecology 136: 1-10. - doi: 10.1016/j.apsoil.2018.

Rocha FI, Jesus EC, Teixeira WG, Lumbreras JF, Clemente EP, Motta PEF, Borsanelli AC, Dutra IS, De Oliveira AP (2023). Soil type determines the magnitude of soil fertility changes by forest-to-pasture conversion in Western Amazonia. Science of The Total Environment 856: 158955. - doi: 10.1016/j.scitotenv.2022.158955

Rufino MPMX, Torres CMME, De Melo FR, De Figueiredo LTM, Da Rocha SJSS, Schettini BLS, Villanova PH, De Freitas MF, Zanuncio JC, Kerkoff LA, Ribeiro FC, Verly OM, Da Silva Costa W (2023). Floristic composition and dispersal syndrome: how can environmental factors affect the Cracidae refuge in a secondary Atlantic Forest fragment? Trees, Forests and People 11: 100374. - doi: 10.1016/j.tfp.2023.100374

Shimamoto CY, Padial AA, Da Rosa CM, Marques MCM (2018). Restoration of ecosystem services in tropical forests: A global meta-analysis. PLoS One 13: 1-16. - doi: 10.1371/journal.pone.0208523 Suarez DR, Rozendaal DMA, De Sy V, Decuyper M, Málaga N, Durán Montesinos P, Arana Olivos A, De la Cruz Paiva R, Martius C, Herold M (2023). Forest disturbance and recovery in Pe-

ruvian Amazonia. Global Change Biology 29: 3601-3621. - doi: 10.1111/gcb.16695

Tenório ARM, Graça JJC, Góes JEM, Mendez JGR, Gama JRNF, Silva PRO, Chagas MPS, Silva RNP, Américo RR, Pereira WLM (1999). Mapeamento dos solos da estação de piscicultura de Castanhal, PA [Mapping of soils at the Castanhal fish farming station, PA]. FCAP, Belém, Brazil, pp. 1-48. [in Portuguese] - doi: 10.5860/choice.41-2927.14

Vasconcelos SS, Zarin DJ, Rosa MBS, Oliveira FA, Carvalho CJR (2007). Leaf decomposition in a dry season irrigation experiment in Eastern Amazonian forest regrowth. Biotropica 35: 593-600. - doi: 10.1111/j.1744-7429.2007.00313.x

Vasconcelos SS, Zarin DJ, Araújo MM, Rangel-Vasconcelos LGT, De Carvalho CJR, Staudhammer CL, Oliveira FDA (2008). Effects of seasonality, litter removal and dry-season irrigation on litterfall quantity and quality in eastern Amazonian forest regrowth, Brazil. Journal of Tropical Ecology 24: 27-38. - doi: 10.1017/S0266467407

Vasconcelos SS, Zarin DJ, Araújo MM, Miranda IS (2012). Aboveground net primary productivity in tropical forest regrowth increases following wetter dry seasons. Forest Ecology and Management 276: 82-87. - doi: 10.1016/j.foreco.20

12.03.034

Villa PM, Ali A, Venncio Martins S, Nolasco De Oliveira Neto S, Cristina Rodrigues A, Teshome M, Alvim Carvalho F, Heringer G, Gastauer M (2020). Stand structural attributes and functional trait composition overrule the effects of functional divergence on aboveground biomass during Amazon forest succession. Forest Ecology and Management 477: 118481. - doi: 10.1016/j.foreco.2020.118481

Villa PM, Martins SV, Rodrigues AC, Safar NVH, Bonilla MAC, Ali A (2019). Testing species abundance distribution models in tropical forest successions: implications for fine-scale passive restoration. Ecological Engineering 135: 28-35. - doi: 10.1016/j.ecoleng.2019.05.015

Wright SJ (2019). Plant responses to nutrient addition experiments conducted in tropical forests. Ecological Monographs 89. - doi: 10.1002/ecm.1382

Zhu X, Jiang X, Kumar Singh A, Zeng H, Chen C, Lu E, Liu W (2022). Reduced litterfall and decomposition alters nutrient cycling following conversion of tropical natural forests to rubber plantations. Ecological Indicators 138: 108819. doi: 10.1016/j.ecolind.2022.108819