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Original Article

Insects, tending ants, and spiders on *Terminalia argentea* (Combretaceae) saplings as bioindicators for the recovery of degraded area

Insetos, formigas cuidadoras e aranhas em mudas de *Terminalia argentea* (Combretaceae) como bioindicadores para a recuperação de área degradada

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Abstract

Anthropogenic activities have intensified soil degradation and disrupted essential ecological processes, underscoring the need for effective ecological restoration strategies. *Terminalia argentea*, a pioneer species of the Cerrado, has demonstrated potential for recovering degraded areas and facilitating arthropod recolonization. Arthropods are sensitive to environmental changes and are thus recognized as bioindicators. This study aimed to assess the recovery of a degraded area by evaluating insect and spider ecological indices, their interactions, and the plant biomass of *T. argentea* saplings over a two-year field establishment period. Saplings with greater biomass (e.g., more leaves/branch) supported a higher abundance and richness of tending ants. During the first year after planting, the leaves of *T. argentea* saplings exhibited higher numbers of chewing insects (e.g., *Cerotoma* sp.) and their ecological indices (e.g., diversity), spiders (e.g., Oxyopidae) and their species richness, bees (e.g., *Trigona spinipes*) and their abundance, and tending ants (e.g., *Brachymyrmex* sp.) and their diversity and richness of species. In contrast, saplings in the second year after planting hosted higher numbers of sap-sucking insects (e.g., *Aphis spiraecola*), their tending ant *Camponotus* sp., and their Dolichopodidae predators. Saplings with more sap-sucking insects (e.g., *Phenacoccus* sp.) also had more tending ants (e.g., *Camponotus* sp.). However, an increase in tending ants (e.g., *Ectatomma* sp.) was associated with a reduction in predators (e.g., *Photinus* sp.) and chewing insects (e.g., *Lamprosoma* sp.). The presence of spiders (e.g., Araneidae) was correlated with higher numbers of chewing insects (e.g., *Cephalocoema* sp.), while *Mantis religiosa* and *Polybia* sp. were more common on saplings with higher defoliation percentages, and *Syrphus* sp. was associated with *Bemisia* sp.. These results indicate that trophic interactions, mediated by both bottom-up and top-down mechanisms, structure the arthropod community on *T. argentea*, promoting the coexistence of functional groups and enhancing ecological indices. Future studies involving predator exclusion and leaf chemical analyses will be essential to deepen this understanding.

Keywords: arthropods, Formicidae, insects, spiders, trophic interactions.

Resumo

As atividades antropogênicas intensificaram a degradação do solo e interromperam processos ecológicos essenciais, ressaltando a necessidade de estratégias eficazes de restauração ecológica. *Terminalia argentea*, uma espécie pioneira do Cerrado, tem demonstrado potencial para a recuperação de áreas degradadas e para facilitar a recolonização por artrópodes. Os artrópodes são sensíveis às mudanças ambientais e, portanto, são reconhecidos como bioindicadores. Este estudo teve como objetivo avaliar a recuperação de uma área degradada por meio da análise de índices ecológicos de insetos e aranhas, suas interações e a biomassa de mudas de *T. argentea* durante um período de dois anos de cultivo em campo. Mudas com maior biomassa (ex.: mais folhas/galho) apresentaram maior abundância e riqueza de formigas cuidadoras. Durante o primeiro ano após o plantio, as folhas das mudas de *T. argentea* apresentaram maior número de insetos mastigadores (ex.: *Cerotoma* sp.) e seus índices ecológicos (ex.: diversidade), aranhas (ex.: Oxyopidae) e sua riqueza de espécies, abelhas (ex.: *Trigona spinipes*) e sua abundância, e formigas cuidadoras (ex.: *Brachymyrmex* sp.) e sua diversidade e riqueza de espécies. Em contraste, as mudas no segundo ano após o plantio apresentaram maior número de insetos sugadores de seiva (ex.: *Aphis spiraecola*), sua formiga cuidadora *Camponotus* sp. e seus predadores da família Dolichopodidae. Mudas com maior número de insetos sugadores de seiva (ex.: *Phenacocus* sp.) também apresentaram maior número de formigas cuidadoras (ex.: *Camponotus* sp.). Contudo, o aumento de formigas cuidadoras (ex.: *Ectatomma* sp.) foi associado à redução de predadores (ex.: *Photinus* sp.) e insetos mastigadores (ex.: *Lamprosoma* sp.). A presença de aranhas (ex.: Araneidae) correlacionou-se com um maior

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número de insetos mastigadores (ex.: *Cephalocoema* sp.), enquanto *Mantis religiosa* e *Polybia* sp. foram mais comuns em mudas com maiores percentuais de desfolha, e *Syrphus* sp. foi associado a *Bemisia* sp.. Esses resultados indicam que as interações tróficas, mediadas por mecanismos ascendentes e descendentes, estruturam a comunidade de artrópodes em *T. argentea*, promovendo a coexistência de grupos funcionais e aprimorando os índices ecológicos. Estudos futuros envolvendo a exclusão de predadores e análises químicas foliares serão essenciais para aprofundar esse entendimento.

Palavras-chave: artrópodes, Formicidae, insetos, aranhas, interações tróficas.

1. Introduction

The restoration of degraded areas is a global challenge, particularly in biomes like the Cerrado, where biodiversity loss and soil degradation are critical (Costa et al., 2020; Oliveira et al., 2020; Rodrigues et al., 2020; Demolin-Leite, 2025). In this context, fertilization with sewage sludge and the introduction of native pioneer species are valuable tools for ecological recovery. These practices enhance soil quality, increase plant biomass, and accelerate restoration, thereby helping to reestablish local and regional ecological functions (Sampaio et al., 2012; Dourado et al., 2020; Silva et al., 2020; Guerrini et al., 2021).

Pioneer plant species such as *Terminalia argentea* Mart. (Combretaceae) are notable for their ability to establish in nutrient-poor, arid soils and to promote natural regeneration and ecosystem stabilization (Lorenzi, 2020; Vieira et al., 2021). Known as "capitão-do-campo," *T. argentea* is a tree native to Brazil, widely used in ecological restoration, landscaping, and timber production (Carvalho et al., 2020; Lorenzi, 2020; Vieira et al., 2021; Leite et al., 2024; Lima et al., 2024a; Longui et al., 2024). Beyond its ecological importance, *T. argentea* possesses medicinal properties derived from secondary metabolites- including phenolic compounds, flavonoids, saponins, tannins, and phytosterols- which can influence its interactions with arthropods (Fahmy et al., 2015; Beserra et al., 2018; Moreira et al., 2020; Venturini et al., 2023).

Arthropods are crucial for maintaining ecological functionality in both natural and restored environments. By acting as herbivores, predators, decomposers, and pollinators, they serve as excellent bioindicators (Sánchez-Bayo and Wyckhuys, 2019). Key groups interacting with *T. argentea* include phytophagous insects, predators, pollinators, tending ants, and spiders (Carvalho et al., 2020; Costa et al., 2021). These interactions are sensitive to factors such as organic fertilization, plant growth stage, and changes in vegetation characteristics like leaf biomass and structural complexity, all of which directly affect resource availability and arthropod community dynamics (El-Shafie, 2022; Demolin-Leite, 2023; Leite et al., 2024; Oliveira et al., 2024). In this context, a *T. argentea* sapling can be conceptualized as a small-scale biogeographic island (Méndez-Castro et al., 2018; Carvalho et al., 2020; Matthews and Triantis, 2021; Al-Namazi and Bonser, 2022; Mech et al., 2024).

Despite their fundamental role, the interactions between *T. argentea* and arthropods, and the effects of the recovery period on these dynamics, remain poorly understood. This study, therefore, aimed to evaluate the restoration of a degraded area by analyzing the ecological indices of insects and spiders (as bioindicators), their trophic interactions, and plant biomass production in *T. argentea* saplings over two years following planting. We tested the following four hypotheses: i) older *T. argentea* saplings will exhibit greater biomass production, thereby making a greater contribution to the recovery of the degraded area; ii) the diversity, richness, and abundance of arthropods will be higher on *T. argentea* saplings with greater biomass; iii) an increase in sap-sucking hemipterans will lead to a greater number of tending ants, which in turn will reduce the numbers of predators and chewing insects; and iv) predators will follow their prey.

2. Material and Methods

2.1. Experimental site

The work was established in a degraded area of the "Instituto de Ciências Agrárias da Universidade Federal de Minas Gerais (ICA/UFMG)" in Montes Claros, Minas Gerais State, Brazil (16° 51' 38" S, 44° 55' 00" W, 620 m.a.l.s.) from April 2020 to March 2022. According to the Köppen climate classification, this area's climate is tropical dry, with annual precipitation between 1000 and 1300 mm, dry winter, and average annual temperature ≥ 26 °C. The soil is Neosol Litolic with an Alic horizon (Silva et al., 2020).

2.2. Experimental design

In March 2019, 24 *T. argentea* seedlings were prepared in a nursery in plastic bags (16 × 24 cm) with reactive natural phosphate mixed with the substrate at a dosage of 160 g. After that, they were planted in the final location in September of the same year. All of them were planted in holes (40 × 40 × 40 cm) when they were 30 cm high, with a 2-m spacing between them. The soil was corrected with dolomitic limestone, increasing base saturation to 50%, natural phosphate, gypsum, FTE (Fried Trace Elements), potassium chloride, and micronutrients equivalent to the needs determined in the soil analysis. A total of 20 L of dehydrated sewage sludge, in a single dose, was placed in each, and the biochemical characteristics of this fertilizer have been reported (Silva et al., 2020). The seedlings were irrigated twice a week until the beginning of the rainy season (October). The design was completely randomized with 24 replications (one sapling each) with first-year and second-year post-planting as treatments.

2.3. Production of vegetal mass and ground cover

The number of leaves/branch and branches/sapling, and the percentage of ground cover by litter, herbaceous, and grassy plants were evaluated visually and monthly per plot ($1m^2$) in the crown projection of each one of the 24 *T. argentea* saplings.

2.4. Counting the arthropods

All insects and spiders were counted, between 7:00 A.M. and 11:00 A.M., by visual observation, every two weeks on the adaxial and abaxial surfaces of the first 12 leaves expanded, per sapling. These leaves were assessed, randomly, on branches (one leaf per position) in the basal, middle, and apical parts of the canopy - vertical axis - (0 to 33%, 33 to 66%, and 66 to 100% of total sapling height, respectively) and in the north, south, east, and west directions- horizontal axis. A total of 12 leaves/sapling/evaluation were observed on 24 *T. argentea* saplings starting six months after transplantation during 24 months (13,824 total leaves), covering the entire sapling (vertical and horizontal axis), capturing the highest possible number of arthropods (insects and spiders), especially the rarest ones. The evaluator approached, carefully, firstly assessing the adaxial leaf surface and, if it was not possible to visualize the abaxial one, with a delicate and slow movement, lifting the leaf to visualize it. Insects with greater mobility (e.g., Orthoptera) that flew, on approach, were counted as long as they were recognized (e.g., Order). The arthropods (insects and spiders) were not removed from the saplings during the evaluation.

A few arthropod specimens (up to 3 individuals) per species were collected using an aspirator (two hours per week) at the beginning of the study (between transplantation and first evaluation, six months after), stored in flasks with 70% alcohol, separated into morphospecies, and sent to specialists for identification (see acknowledgments). Any visible arthropod, not yet computed in previous evaluations, was collected, coded, and sent to a taxonomist of its group.

2.5. Statistical analysis

Each replication is the total of individuals collected on 12 leaves (three heights and four sides of the sapling). The ecological indices (abundance, diversity, and species richness) were calculated per group (e.g., chewing insects) and treatments (first and second year after planting) using the BioDiversity Professional, *version* 2 (© 1997). Abundance and species richness were the total numbers of individuals and species, respectively, per sapling. Diversity was calculated using the Hill' formula (1st order): N1= exp (H'), where H' is the Shannon-Weaver diversity index, calculating the diversity with the actual species number.

The data for abundance, diversity, and species richness of phytophagous insects, pollinators, and natural enemies were subjected to a non-parametric statistical hypothesis, the Wilcoxon signed rank test (p-value< 0.05) using the Statistics and Genetics Analysis (SAEG) program, version 9.1. The data were subjected to second-degree regression or principal component regression (PCR), when linear (p-value< 0.05) to verify the possible interactions (e.g., protocooperation) between groups of arthropods (e.g., spiders). All arthropods sampled were included in the analyses.

Simple equations were selected based on the criteria: i) distribution of the data in the figures (linear or quadratic response), ii) the parameters used in these regressions were the most significant ones (p-value< 0.05), iii) p-value < 0.05 and *F* of the Analysis of Variance of these regressions, and iv) the determination coefficient of these equations (R^2). The PCR model uses principal component analysis to obtain the regression based on a covariance matrix. These reduce the regression dimensions, excluding those that contribute to collinearity, that is, linear relations between the independent variables. The parameters used in these equations were all significant (p-value<0.05) according to the selection of the variables by the "Stepwise" method using the statistical program mentioned. The data presented are the significant ones (p-value<0.05) (Tables 1 to 3), and the others are in Supplementary Material I.

3. Results

3.1. Plant biomass production and defoliation

The number of leaves/branch on *T. argentea* saplings decreased in the second year after planting (Table 1). Saplings with a higher number of leaves/branch supported a greater number of *Ectatomma* sp., *Pheidole* sp. (Hymenoptera: Formicidae), as well as higher overall abundance and richness of tending ants. Furthermore, saplings with more branches/sapling exhibited a higher number of *Camponotus* sp. and *Euxesta* sp. (Diptera: Otitidae) (Table 2). Increased defoliation was positively correlated with the species richness of chewing insects and with the number of *Trigona spinipes* (Apidae: Hymenoptera).

3.2. Arthropods and their ecological indices

In the first year after planting, the leaves of *T. argentea* saplings supported a higher number of several arthropod groups and their ecological indices. These included i) chewing insects, *Psiloptera* sp. (Coleoptera: Buprestidae), *Cerotoma* sp. and *Lamprosoma* sp. (Coleoptera: Chrysomelidae), *Diorymerus* sp. (Coleoptera: Curculionidae), and caterpillars (Lepidoptera). The overall abundance, diversity, and species richness of this group were also higher. ii) natural enemies: Oxyopidae (Araneae), *Photinus* sp. (Coleoptera: Lampyridae), *Polybia* sp. (Hymenoptera: Vespidae). Spider species richness was also elevated. iii) pollinators: *Trigona spinipes* (Hymenoptera: Apidae), along with a higher overall abundance of pollinators. And iv) tending ants: *Brachymyrmex* sp., *Ectatomma* sp., *Pheidole* sp., and *Pseudomyrmex termitarius* (Hymenoptera: Formicidae). This group also exhibited greater diversity and species richness. Conversely, the second year after planting was characterized by higher numbers of different groups, specifically: i) herbivorous insects: Clytrini (Coleoptera: Chrysomelidae), *Euxesta* sp. (Diptera: Otitidae), and *Aphis spiraecola* (Hemiptera: Aphididae); ii) predators: Dolichopodidae (Diptera); and iii) tending ants: *Camponotus* sp. (Hymenoptera: Formicidae) (Tables 1 and 3).

3.3. Ecological relationships among arthropod groups

A mutualistic relationship was observed between the tending ant *Camponotus* sp. and the sap-sucking hemipterans *Phenacoccus* sp. and *A. spiraecola*, where increases in one group corresponded to increases in the other on *T.*

Table 1. Abundance (Abun.), Diversity (D.) and species richness (S.R) of phytophagous chewing insects (Chew.), Hemiptera phytophagous (Hem.), pollinators (Poll.), tending ants (Ants), Sternorrhyncha predators (Pred.), spiders (Spid.), number of branches/sapling and leaves/branch, percentages of defoliation by insects and ground cover per *Terminalia argentea* (Combretaceae) sapling (mean ± SE) and planting year.

Variables	Year		TW*	
	First	Second	VT^{ε}	*P*
Abun. Chew.	7.58 ± 1.10	3.50 ± 0.57	2.68	0.00
D. Chew.	7.77 ± 1.10	4.61 ± 0.73	2.03	0.02
S.R. Chew.	3.58 ± 0.37	2.25 ± 0.27	2.50	0.00
Abun. Hem.	5.63 ± 2.80	15.42 ± 8.14	0.31	0.37
D. Hem.	1.23 ± 0.37	1.25 ± 0.45	0.00	0.50
S.R. Hem.	1.08 ± 0.19	0.88 ± 0.21	0.94	0.17
Abun. Poll.	8.71 ± 2.64	1.63 ± 0.55	1.98	0.02
D. Poll.	0.48 ± 0.14	0.57 ± 0.17	0.20	0.42
S.R. Poll.	0.63 ± 0.10	0.50 ± 0.13	1.05	0.14
Abun. Ants	16.42 ± 2.85	12.25 ± 1.86	0.87	0.19
D. Ants	4.64 ± 0.49	2.41 ± 0.25	3.48	0.00
S.R. Ants	2.83 ± 0.17	1.71 ± 0.18	3.78	0.00
Abun. Pred.	1.46 ± 0.41	1.83 ± 0.31	1.41	0.07
D. Pred.	1.03 ± 0.26	1.05 ± 0.25	0.03	0.48
S.R. Pred.	0.83 ± 0.13	0.96 ± 0.12	0.70	0.24
Abun. Spid.	1.42 ± 0.29	2.96 ± 1.41	1.08	0.14
D. Spid.	1.27 ± 0.49	0.61 ± 0.23	0.42	0.33
S.R. Spid.	1.25 ± 0.22	0.67 ± 0.14	1.89	0.02
Leaves/branch	12.05 ± 0.39	10.61 ± 0.33	2.66	0.00
Branches/sapling	27.44 ± 1.34	29.59 ± 2.04	0.85	0.19
Ground cover	10.65 ± 0.97	14.89 ± 2.15	0.78	0.21
Defoliation	8.47 ± 0.45	7.62 ± 0.27	1.16	0.12

*TW = Test of Wilcoxon; $^{\varepsilon}$VT = value of test; n = 24 per treatment.

argentea saplings. The presence of certain tending ants had suppressive effects on other arthropods. A higher number of *Ectatomma* sp. and *Pheidole* sp. was associated with reduced numbers of the predators *Photinus* sp. and *Polybia* sp., respectively. Furthermore, *Pheidole* sp. was negatively associated with the phytophagous insects *Lamprosoma* sp., *Tropidacris collaris* (Orthoptera: Romaleidae), and Pentatomidae (Hemiptera), as well as with the overall abundance of chewing insects. Similarly, *P. termitarius* and *Camponotus* sp. were linked to decreases in *Epitragus* sp. (Coleoptera: Tenebrionidae) and *Euxesta* sp., respectively. In general, a greater abundance and diversity of tending ant species were associated with reduced abundance of chewing insects (Table 2).

Predator abundances were positively linked to the availability of their prey. Saplings with higher numbers of the chewing insects Cerambycidae (Coleoptera) and *Cephalocoema* sp. (Orthoptera: Proscopiidae) supported increased numbers of Araneidae and a higher overall spider abundance. Similarly, increases in Oxyopidae were associated with more *Cerotoma* sp. and *Diorymerus* sp.. The number of the predator *Mantis religiosa* (Mantodea: Mantidae) increased with higher numbers of the phytophagous insects Phaneropterinae (Orthoptera: Tettigoniidae) and Fulgoridae (Hemiptera), the predator *Cycloneda sanguinea* (Coleoptera: Coccinellidae), and with the percentage of defoliation. The number of the predator *Polybia* sp. was also higher on saplings with greater defoliation, a higher overall abundance of chewing insects, and more Fulgoridae. Finally, the number of *Syrphus* sp. (Diptera: Syrphidae) was positively correlated with that of *Bemisia* sp. (Hemiptera: Aleyrodidae) (Table 2).

4. Discussion

In the second year after planting, *T. argentea* saplings exhibited a reduction in the number of leaves/branch. This finding does not support our first hypothesis, which proposed that older saplings would have greater plant biomass production. The sustained vertical growth and maintained vegetation cover between the first and second years were likely facilitated by fertilization with sewage

Table 2. Relationships between abundance (Abun.) of chewing insects (Chew.), phytophagous Hemiptera (Hem.), tending ants (Ants), and spiders (Spid.), diversity (D.) of ants, and species richness (S.R) of ants and Chew., numbers of *Aphis spiraecola* (Aphis), Araneidae (Aran.), *Bemisia* sp. (Bemi.), *Camponotus* sp. (Camp.), Cerambycidae (Ceram.), *Cerotoma* sp. (Cero.), *Cephalocoema* sp. (Cephal.), *Cycloneda sanguinea* (Csang.), *Diorymerus* sp. (Diory.), *Ectatoma* sp. (Ecta.), *Epitragus* sp. (Epi.), *Euxesta* sp. (Eux.), Fulgoridae (Fulg.), *Lamprosoma* sp. (Lampr.), *Mantis religiosa* (Mrel.), Oxyopidae (Oxyo.), Pentatomidae (Pent.), *Phenacoccus* sp. (Phen.), *Pheidole* sp. (Phei.), *Photinus* sp. (Phot.), *Polybia* sp. (Poly.), *Pseudomyrmex termitarius* (Pter.), *Syrphus* sp. (Syrp.), Phaneropterinae (Phan.), *Trigona spinipes* (Tspi.), *Tropidacris collaris* (Tcoll.), percentage of defoliation (Def.), branches/sapling (Branches), and leaves/branch (Leaves) on *Terminalia argentea* (Combretaceae) saplings.

Principal component regressions	R^2	*F*	*P*
Abun.Spid=1.01+7.12xCeram.+3.50xCephal.	0.45	18.59	0.00
Aran.=0.24+7.44xCeram.+3.69xCephal.	0.50	22.24	0.00
Camp.=-3.16+2.58xPhen.+0.26xBranches+0.08xAphis	0.42	10.76	0.00
Def.=6.79+S.R.Chew.+0.10xTspi.	0.38	13.54	0.00
Mrel.=-0.41+0.44xCsang.+0.21xPhan.+0.07xFulg.+0.05xDef.	0.59	15.64	0.00
Poly.=-0.57+0.08xDef.+0.07xFulg.+0.04xAb.Chew.	0.34	7.57	0.00
First and Second degree regressions			
Ab.Ants=-15.32+2.62xLeaves	0.18	10.00	0.00
Ab.Chew.=2.02+0.36xAb.Ants-0.005xAb.Ants^2	0.18	4.82	0.01
Ab.Chew.=0.72+2.21xD.Ants-0.17xD.Ants^2	0.14	3.75	0.03
Ab.Chew.=4.31+0.65xPhei-0.01xPhei.^{2}	0.16	4.37	0.01
Ab.Hem.=3.89+1.25xCamp.	0.11	5.88	0.01
S.R.Ants=0.08+0.19xLeaves	0.13	6.58	0.01
Aphis=1.93+1.21xCamp.	0.10	5.36	0.02
Ecta.=-6.89+0.71xLeaves	0.19	10.67	0.00
Epi.=0.04+0.18xPter.-0.01xPter.^{2}	0.16	4.35	0.01
Eux.=0.05+0.07xCamp.-0.002xCamp.^{2}	0.14	3.75	0.03
Eux.=-0.40+0.02xBranches	0.11	5.67	0.02
Lampr.=0.54+0.15xPhei-0.003xPhei.^{2}	0.18	4.89	0.01
Oxyo.=0.16+0.23xCero.	0.13	7.13	0.01
Oxyo.=0.15+0.10xDiory.	0.14	7.42	0.00
Pent.=0.13+0.09xPhei-0.002xPhei.^{2}	0.16	4.24	0.02
Phei.=-15.74+1.67xLeaves	0.18	10.40	0.00
Phen.=-0.26+0.09xCamp.	0.24	14.33	0.00
Poly.=0.22+0.09xPhei-0.002xPhei.^{2}	0.16	4.32	0.01
Phot.=0.08+0.23xEcta.-0.02xEcta.^{2}	0.13	3.34	0.04
Syrp.=0.06+0.09xBemi.	0.21	11.90	0.00
Tcoll.=0.61+0.23xPhei-0.005xPhei.^{2}	0.15	3.88	0.02

n = 48.

sludge, a rich source of macro- and micronutrients such as nitrogen, phosphorus, and potassium (Costanzo et al., 2021). Sewage sludge has been shown to promote increased biomass and accelerated growth in various plant species, including *Brassica napus* (Brassicaceae), *Eucalyptus grandis* (Myrtaceae), *Helianthus annuus* (Asteraceae), *Miscanthus giganteus* (Poaceae), and *Zea mays* (Poaceae) (Silva et al., 2011; Dubis et al., 2020; Kominko et al., 2022). As pioneer species like *T. argentea* respond rapidly to nutrient availability, they often prioritize structural growth and height gain over leaf production and longevity (Coll et al., 2008; Selaya and Anten, 2010; Bardy et al., 2023; Shannon et al., 2023). Furthermore, competition for light within the developing canopy can drive the reallocation of resources to new, higher tissues. This accelerates the senescence of lower, shaded leaves and favors monopodial growth, thereby promoting more efficient light capture (Selaya and Anten, 2010). Therefore, the observed reduction in leaf biomass in *T. argentea* likely reflects a strategic physiological (e.g., trade-off between growth and leaf maintenance) adjustment to support

Table 3. Order, family, and species of spiders (Class Arachnidae) and insects (Class Insecta) per *Terminalia argentea* (Combretaceae) sapling (mean ± SE) and planting year.

Order: Family: Specie	Year		TW*	
	First	Second	VT^{ε}	*P*
Ara.: Oxyopidae: Not identified	0.33 ± 0.11	0.08 ± 0.05	1.86	0.03
Col.: Buprestidae: *Psiloptera* sp.	0.21 ± 0.13	0.00 ± 0.00	1.77	0.03
Chrysomelidae: Clytrini	0.04 ± 0.04	0.21 ± 0.08	1.73	0.04
Cerotoma sp.	0.46 ± 0.19	0.00 ± 0.00	2.59	0.00
Lamprosoma sp.	1.21 ± 0.21	0.42 ± 0.15	3.09	0.00
Curculionidae: *Diorymerus* sp.	1.17 ± 0.48	0.00 ± 0.00	2.59	0.00
Lampyridae: *Photinus* sp.	0.33 ± 0.15	0.00 ± 0.00	2.33	0.00
Dip.: Dolichopodidae: Not identified	0.75 ± 0.41	1.63 ± 0.28	3.22	0.00
Otitidae: *Euxesta* sp.	0.04 ± 0.04	0.38 ± 0.14	2.31	0.01
Hem.: Aphididae: *Aphis spiraecola*	2.83 ± 2.83	13.88 ± 8.18	1.95	0.02
Hym.: Apidae: *Trigona spinipes*	8.67 ± 2.64	1.50 ± 0.51	1.97	0.02
Formicidae: *Brachymyrmex* sp.	3.75 ± 1.08	1.38 ± 0.52	1.79	0.03
Camponotus sp.	0.13 ± 0.06	10.50 ± 1.78	5.64	0.00
Ectatoma sp.	2.25 ± 0.85	0.04 ± 0.04	3.81	0.00
Pheidole sp.	6.25 ± 1.97	0.13 ± 0.06	5.05	0.00
Pseudomyrmex termitarius	4.04 ± 1.01	0.17 ± 0.09	4.20	0.00
Vespidae: *Polybia* sp.	0.63 ± 0.15	0.13 ± 0.06	2.83	0.00
Lep.: Not identified	0.25 ± 0.09	0.04 ± 0.04	2.02	0.02

*TW= Test of Wilcoxon; $^{\varepsilon}$VT= value of test; *n* = 24 per treatment.

sustained vertical growth rather than a simple loss of biomass (source-drain relationship).

In the first year after planting, the leaves of *T. argentea* saplings supported higher numbers of chewing insects (e.g., *Psiloptera* sp.), spiders (e.g., Oxyopidae), bees (e.g., *T. spinipes*), and tending ants (e.g., *Brachymyrmex* sp.), as well as greater ecological indices (e.g., abundance, diversity, or species richness) for these groups. These patterns are consistent with the Theory of Island Biogeography (BGI). According to this theory, increased plant biomass (e.g., more leaves/branch) expands the availability of resources such as food and shelter, creating more niches and microhabitats, thereby supporting a greater "carrying capacity" for arthropods (Silva et al., 2020, 2021; Mota et al., 2023; Souza et al., 2023). This condition facilitates higher arthropod ecological indices, as previously documented for *T. argentea* (Carvalho et al., 2020; Costa et al., 2021), and favors the diversity of herbivores and tending ants, which in turn supports their natural enemies (Leite et al., 2016, 2017, 2024; Macedo-Reis et al., 2019; Oliveira et al., 2024). These findings support hypothesis ii, which predicted that arthropod diversity, richness, and abundance would be higher on *T. argentea* saplings with greater biomass. Furthermore, this ecological cascade was likely initiated by the accelerated growth of saplings promoted by nitrogen-rich sewage sludge fertilization (Wierzbowska et al., 2021). Beyond simply increasing biomass, fertilization enhanced host plant quality by improving palatability (e.g., reducing leaf toughness) (Zeng et al., 2024) and nutritional value (e.g., elevating free amino acid levels) (Cristina et al., 2020; Lee et al., 2021). This improvement in host quality intensified colonization by herbivorous insects and, consequently, by their associated arthropod communities on the more robust *T. argentea* saplings.

In the second year after planting, an increase in the abundance of sap-sucking hemipterans (e.g., *A. spiraecola*) was accompanied by a rise in their tending ant, *Camponotus* sp. Conversely, saplings with a higher number of other tending ants (e.g., *Ectatomma* sp.) supported fewer predators (e.g., *Polybia* sp.) and chewing insects (e.g., *T. collaris*). These findings confirm our third hypothesis that an increase in sap-sucking hemipterans would lead to greater numbers of tending ants, which in turn would reduce populations of predators and chewing insects on *T. argentea*. These patterns result from mutualistic interactions, where ants protect sap-sucking hemipterans from natural enemies in exchange for honeydew, while also directly suppressing herbivores through top-down control, thereby reducing defoliation (Venturino et al., 2008; Vidal and Murphy, 2018; Camacho and Avilés, 2021; Nelson and Mooney, 2022). Similar trophic outcomes have been documented for *Acacia auriculiformis* (Mota et al., 2023; Teixeira et al., 2024), *Acacia mangium* (Lima et al., 2024b), *Caryocar brasiliense* (Demolin-Leite et al., 2024), *Sapindus saponaria* (Souza et al., 2023; Demolin-Leite, 2024), and *T. argentea* (Carvalho et al., 2020; Costa et al.,

2021). Collectively, these findings underscore the critical role of such interactions in the establishment, stability, and maintenance of arthropod communities (Schmitz and Barton, 2013; Pettorelli et al., 2015).

The fourth hypothesis- that predator abundance follows prey availability- was confirmed. This was evidenced by several specific relationships: higher numbers of spiders (e.g., Oxyopidae) on *T. argentea* saplings were associated with increased numbers of chewing insects (e.g., *Cerotoma* sp.); higher numbers of prey (e.g., Phaneropterinae) and related herbivory indices (e.g., percentage of defoliation) led to more *M. religiosa*; and increased numbers of *Bemisia* sp. resulted in more *Syrphus* sp.. The greater structural complexity generated by increased sapling biomass directly benefits predators such as spiders. Plant architecture provides essential web support and modulates microhabitat conditions, thereby influencing spider diversity and community composition (Uetz, 1991; Langellotto and Denno, 2004). This relationship is functionally critical, given the role of spiders as obligate predators (Landis et al., 2000; Lang, 2003; Venturino et al., 2008; Leite et al., 2012; Silva et al., 2020). These findings highlight an interplay between bottom-up and top-down forces. A bottom-up effect, where plant complexity creates niches for various herbivore and predator guilds (Filloy et al., 2023; Pequeno et al., 2023), is coupled with top-down control, where predators (e.g., spiders, wasps, and mantids) regulate prey populations (Michelutti et al., 2017; Michalko et al., 2019; Rankin et al., 2023). Consequently, the correlation between phytophagous insects and their predators demonstrates that trophic interactions respond dynamically to resource availability. This dynamic promotes cascading effects that regulate the community, facilitate the coexistence of different functional groups, and sustain high ecological indices (Halaj and Wise, 2001; Klauschies et al., 2016; Vidal and Murphy, 2018; Iwashita et al., 2022; Saha et al., 2023).

5. Conclusions

The structure of the arthropod community on *T. argentea* saplings is shaped by a complex interplay between the plant's growth strategy and resultant trophic cascades. The rejection of the first hypothesis reveals a key physiological adjustment in the plant, favoring competitive vertical growth over simple foliar biomass accumulation. Despite this, initial sewage sludge fertilization initiated strong bottom-up effects, confirming that greater plant biomass enhances arthropod ecological indices (supporting hypothesis ii). Subsequent trophic interactions- including mutualism between tending ants and sap-sucking hemipterans, and classic predator-prey dynamics- were fundamental to community regulation, thereby confirming hypotheses iii and iv and underscoring the role of top-down control. Our findings demonstrate that both bottom-up and top-down processes are pivotal in structuring arthropod communities within recovering ecosystems. Future research should employ predator exclusion experiments and plant tissue chemical analyses to further elucidate the mechanisms driving these community dynamics throughout ecological succession.

Data Availability Statement

The entire data set supporting the results of this study has been published in the paper itself.

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Supplementary Material

Supplementary material accompanies this paper.

Supplementary material I. Order, family, and species of spiders (Class Arachnidae) and insects (Class Insecta) per Terminalia argentea (Combretaceae) sapling (mean ± SE) and planting year.

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