




## Article

# Litter Deposition and Nutrient Cycling of Invaded Environments by *Cryptostegia madagascariensis* at Tropical Cambisols from Northeastern Brazil

Tancredo Souza <sup>1,2,\*</sup> , Edjane Oliveira de Lucena <sup>2</sup> , Leonaldo Alves de Andrade <sup>3</sup>,  
Lucas Jónatan Rodrigues da Silva <sup>4</sup>, Gislaïne dos Santos Nascimento <sup>2</sup>  and Helena Freitas <sup>1</sup>

<sup>1</sup> Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, 3000-456 Coimbra, Portugal

<sup>2</sup> Postgraduate Program in Soil Science, Department of Soils and Rural Engineering, Federal University of Paraíba, Areia 58397-000, Paraíba, Brazil

<sup>3</sup> Postgraduate Program of Soil Science, Department of Soils and Rural Engineering, Federal University of Paraíba, Areia 58397-000, Paraíba, Brazil

<sup>4</sup> Postgraduate Program in Agrarian and Natural Ecosystems, Department of Agriculture, Biodiversity and Forests, Federal University of Santa Catarina, Curitibanos 89520-000, Santa Catarina, Brazil

\* Correspondence: tancredo\_agro@hotmail.com; Tel.: +55-83-999-930-306

**Abstract:** *Cryptostegia madagascariensis* is an invasive plant species that covers 11% of the Brazilian northeastern territory, but its role on the litter trait in tropical ecosystems remains unclear. Here, we analyzed and compared the litter deposition, litter nutrient content, soil organic matter, and the litter decay rate from invaded and non-invaded environments by *C. madagascariensis* at a tropical Cambisol. The PCA analysis revealed that litter deposition, litter quality, and soil organic matter were correlated with the invaded environment. We grew plant species in greenhouse conditions to obtain a standard litter material to use in our litter bags in field conditions. We found that litter decay rate was higher in the invaded environment than in the non-invaded one. Our results suggest that *C. madagascariensis* changes litter traits in tropical ecosystems that in turn create negative plant–soil feedback to the native species by creating a physical barrier on soil surface and to promote its own rhizosphere.

**Keywords:** Caatinga ecoregion; invasive plant species; litter decomposition; litter decay rate; litter traits



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## 1. Introduction

Invaded environments by invasive plant species are characterized by changes in soil organic matter, litter decomposition, litter decay rate, and litter macronutrient contents, as a strategy of invasive plant species' spread, growth, development, and reproduction [1,2]. In tropical ecosystems, the biological invasion promoted by *Cryptostegia madagascariensis* is influenced by the continuous litter input of the invader, which promotes drastic changes into the soil ecosystem by increasing the soil organic carbon over time [3]. Overall, the effects of biological invasion by *C. madagascariensis* and its mechanisms underlying invasion success have been previously described in semi-arid ecosystems [4,5]. Caatinga, an important ecoregion of Brazil, is affected by an invasive species, *Cryptostegia madagascariensis* Bojer ex Decne, imported due to its ornamental uses. The invader establishes dense aboveground stands across the tropical ecosystems [5]. Its occurrence has been described in 11% of the Brazilian northeastern territory, mainly in the states of Ceara and Paraíba [3]. The state of Paraíba is divided into four major regions (e.g., “Zona da Mata”, “Agreste”, “Borborema”, and “Sertão”), and the invasive plant species occurs in 23.7% of the region of “Sertão” (that corresponds to 40.23% of total state area) [4]. This invasive plant species promotes changes in soil chemical properties (e.g., soil pH, soil nutrient contents, and soil organic matter) [3], thus creating positive plant–soil feedback for its own benefit during

the biological invasion [6]. Its morphological and anatomical traits have negative effects on seed bank diversity and native plant species growth, thus creating negative plant-soil feedback for the native plant species [3,5].

Tesfaye et al. [2] have reported high soil organic matter contents in tropical environments that present high litter deposition. On the one hand, this phenomenon may improve net primary production [7,8]. On the other hand, the high litter deposition may create a physical barrier that negatively affects native soil seed bank overtime [9]. Litter material with different composition may present a dissimilar decomposition rate (e.g., high lignin content is related to low decomposition rate) [10]. Some studies have reported faster litter decomposition in invaded environments when compared to the non-invaded environments [11,12]. However, litter deposition, litter quality, and litter decomposition from invaded environments in a tropical ecosystem are rare and poorly described. It remains unclear if *C. madagascariensis* changes the litter compartment in tropical ecosystems. Thus, as far as we know, this is the first report showing changes on litter deposition, litter quality, and soil organic matter of tropical Cambisols invaded by *C. madagascariensis*.

Studies considering the biological invasion process by *Cryptostegia madagascariensis* in tropical Cambisols are rare [13]. In general, tropical Cambisols present high acid levels, low soil fertility, high plant species diversity, and high endemism, and some plant species are classified as endangered plant species [14,15]. In addition, seasonal variation (e.g., rainy vs. dry seasons) can contribute to the biological invasion process [10]. This phenomenon supports the “seasonal priority effects” hypothesis [16]. According to this theory, phenological traits of some invasive plant species can optimize the invasive competitiveness, rapid growth, availability of light, nutrients acquisition, and attract pollinators on a seasonal scale within the year [17]. Therefore, we hypothesized that *C. madagascariensis* can promote changes in the environment by altering litter deposition, soil organic matter, and litter decay rate.

We aimed to determine whether *C. madagascariensis* invasion in a native environment influences: (i) litter deposition; (ii) soil physical–chemical properties (e.g., soil temperature, soil water content, and soil organic matter); (iii) litter nutrient content (e.g., N, P, K); and (iv) litter decay rate in a tropical Cambisol. We expected to characterize the soil ecosystem [18] to assess the litter biomass by estimating litter inputs [19] and to characterize the litter chemical composition to understand nutrient cycling in invaded and non-invaded environments [20].

## 2. Materials and Methods

### 2.1. Studied Plant Species

*Cryptostegia madagascariensis* is a native plant species from Madagascar island. This plant species was introduced worldwide and has become an invasive plant species in some countries (e.g., Australia, Brazil, and Hawaii) due to its ornamental uses. It can grow in tropical environments where it can access full sunlight. In the Brazilian northeast, it is considered a serious invasive plant species due to its capacity to establish dense stands, promoting negative impacts on native vegetation such as: (i) native seed bank and plant species diversity reduction [3,4], (ii) changes in soil chemical properties (e.g., soil organic carbon) [3], and (iii) reduction of sunlight to native plant species [5].

*Mimosa tenuiflora* (Willd.) Poir is a native plant species from the Brazilian xeric shrubland that has an important ecological and cultural role in the Brazilian northeastern culture (among afro-descendant and indigenous groups). It shows high rusticity, rapid growth, and it is considered a prolific pioneer. Some studies have reported this native plant species with 47% of relative dominance and have described *M. tenuiflora* as an important plant species for caatinga reforestation [3]. According to Alves et al. [21], during the dry season, its leaves start to fall, representing an adaptive strategy to save energy and to survive in tropical environments. In the sites of non-invaded environments, the mean relative dominance of *M. tenuiflora* was 47%. Thus, we selected this native plant species as a model plant to characterize the litter deposition and nutrient cycling

in the non-invaded environment. It enabled us to compare the results from an invaded environment by *C. madagascariensis* and a non-invaded environment with significant relative dominance of *M. tenuiflora*.

## 2.2. Study Sites and Experimental Design

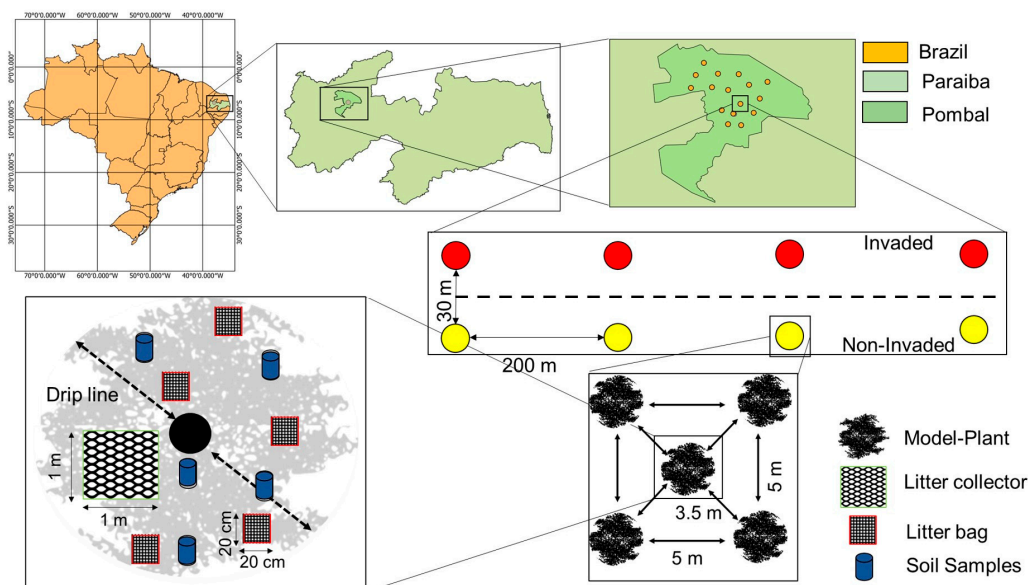
This study was conducted in two riparian habitats near Piancó River Basin (6°47'34.1" S and 37°49'10.7" W) at 156 m.a.s.l. in Pombal, Paraiba, Brazil: (a) an invaded environment dominated by the invasive plant species *Cryptostegia madagascariensis* (relative dominance = 80%); and (b) a non-invaded environment characterized by the presence of native plant species such as: *Mimosa tenuiflora* (Wild) Poir, *Aspidosperma pyrifolium* Mart. & Zucc, *Croton sonderianus* Muell. Arg., *Cereus jamacaru* DC., *Jatropha mollissima* (Pohl) Baill., *Melocactus zehntneri* (Britton & Rose) Luetzelburg, *Poincianella pyramidalis* (Tul.) L.P. Queiroz, *Urtica dioica* L., and *Sarcomphalus joazeiro* (Mart.) Hauenschild. In this environment, we selected *M. tenuiflora* as the model plant due to its relative dominance (e.g., 47%). The invasive and native plant species grew from May 2017 (early rainy season) to August 2018 (early dry season). The climate is a classified BSh-type (hot semi-arid climate) according to the Köppen climate classification. The total annual precipitation and annual mean air temperature are 963.07 mm and +28 °C, respectively. The soil type of both environments was classified as Cambisol with clay texture [22]. More details about the biodiversity indices of plant community composition and soil characterization of both studied environments are described in Table 1.

**Table 1.** Biodiversity indices of plant community composition and soil characterization (mean, N = 16) in both invaded and non-invaded environments in a tropical Cambisol, Caatinga ecoregion, Paraiba, Brazil.

Studied Environments	Species Richness (S)	Shannon's Diversity Index	Clay Content (g kg <sup>-1</sup> )	Soil pH (1:2.5 Soil:Water, v:v)	Total Nitrogen (g kg <sup>-1</sup> )	Available P (mg kg <sup>-1</sup> )	K <sup>+</sup> (mg kg <sup>-1</sup> )	Ca <sup>2+</sup> (cmol <sub>c</sub> kg <sup>-1</sup> )	Mg <sup>2+</sup> (cmol <sub>c</sub> kg <sup>-1</sup> )
1-10 Invaded environment	5 (1)	1.17 (0.23)	634.0 (23.0)	5.85 (1.18)	0.60 (0.04)	246.16 (1.06)	132.28 (0.75)	7.04 (0.13)	6.50 (0.67)
Non-invaded environment	20 (3)	2.72 (0.45)	631.0 (36.0)	6.00 (0.57)	0.10 (0.05)	200.16 (1.04)	125.18 (3.16)	5.85 (0.15)	6.05 (0.29)

The standard deviation is shown in parentheses.

We selected 16 sites within the studied area. In addition, in each site, we placed 30 m transects with four sampling points between the invaded environment and the non-invaded one (each transect was located 200 m apart from each other) (Figure 1). Around each sampling point, five model plants were selected according to the following criteria: (a) the plant species had a diameter near the soil surface > 3 cm; (b) the plant species had a height higher than 2 m; (c) in the flowering stage; and (d) no individuals from a different plant species were growing in a 3 m radius from the selected plant in all directions [6]. We collected samples from one litter collector, five litterbags, and five soil samples by the model plant. We used the litter collectors to determine litter deposition and litter nutrient contents (e.g., N, P, and K). The litterbags (e.g., 50 g of litter material) were used to compare litter decay rate, and soil samples were used to characterize soil properties.



**Figure 1.** Location and experimental design of each studied transect into the experimental area, Pombal, Paraíba, Brazil. Non-invaded and invaded environments were examined within each environment. Inset shows the studied transects.

### 2.3. Litter Deposition

We collected samples from the litter collectors ( $1 \times 1$  m, with a  $2 \times 2$  mm nylon mesh-type) by each model plant to determine the litter deposition during the rainy and dry seasons. The litter collectors were placed below the drip line of each model plant. In total, we placed 64 litter collectors (16 sites  $\times$  4 sampling points) in the studied environments. The litter material on each collector was sampled following a schedule of 60 days during the whole experiment [23]. All litter material was oven dried at  $65^\circ\text{C}$  for 48 h and weighed to estimate litter dry deposition ( $\text{kg ha}^{-1}$ ) by using the following equation: Litter dry deposition ( $\text{kg ha}^{-1}$ ) = Litter dry deposition ( $\text{kg m}^{-2}$ )  $\times$  10,000 [24].

### 2.4. Litter Quality and Soil Properties

We analyzed litter N, P, and K contents from the litter material samples in each litter collector during the rainy and dry seasons. The litter N content was determined using Kjeldahl's protocol [25]. The vanadate molybdate colorimetric method was used to determine the litter P content. The litter K content was determined by atomic absorption spectrophotometer. Finally, we analyzed the soil temperature, soil water content, and soil organic matter. All analyses were performed following the protocol [26].

### 2.5. Litter Preparation

In greenhouse conditions, the litter decomposition of six native species was analyzed and compared with the invasive one. To prepare the litter material, six native plant species (*M. tenuiflora*, *A. yrifolium*, *C. sonderianus*, *J. mollissima*, *P. pyramidalis*, and *S. joazeiro*) were grown together in plastic pots containing 4 L of autoclaved sand under greenhouse conditions ( $25:20^\circ\text{C}$  day: night temperature) for 8 weeks. Briefly, seeds were surface sterilized with 0.5% NaOCl. To collect the aboveground plant, litter shoots were cut a surface level. Plant biomass was dried at  $40^\circ\text{C}$ . The litter material used in the litter decomposition assay comprised freshly cut dried material rather than naturally senesced plant material. We characterized lignin content, total organic carbon, nitrogen content, and phosphorous content from the standard litter material (Table 2).

**Table 2.** Lignin and nutrient contents from the standard litter material used in the litter decomposition assay (mean  $\pm$  standard deviation,  $N = 25$ ).

Lignin (%)	TOC (%)	N (%)	P (mg kg <sup>-1</sup> )
47.9 $\pm$ 0.8	24.7 $\pm$ 2.5	2.11 $\pm$ 0.11	63.8 $\pm$ 6.8

Litter lignin and nutrient contents were determined following the protocols [26]. TOC, total organic carbon.

### 2.6. Litter Decomposition (Litter Decay Rate)

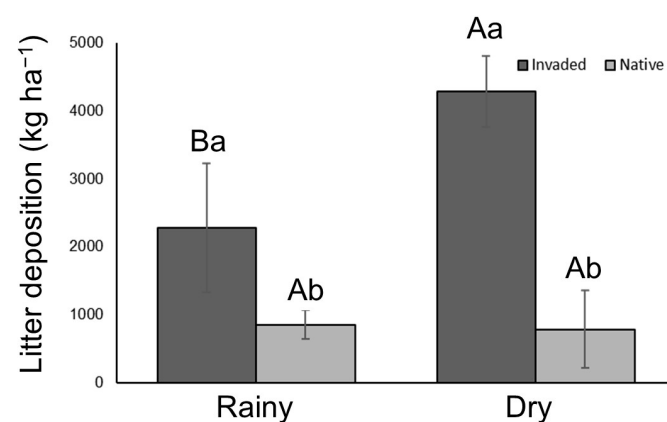
We used the litterbags (20  $\times$  20 cm, with 2 mm mesh-type) to determine the litter decay rate ( $k$ ), half decay time ( $hd$ ), and total decay time ( $td$ ). Each litterbag received 50 g of dry litter material that we previously collected from each environment. The litterbag assay followed a schedule of 60 days for 10 months. The remain litter material collected in each litterbag was oven dried at 60 °C to determine the remaining litter dry biomass. First, the litter decay rate ( $k$ , years<sup>-1</sup>) was determined using the following equation:  $x/x_0 = e^{-kt}$ , where  $x$  (g) is the remaining biomass after  $t$  years (1/6 years), and  $x_0$  (g) is the initial litter biomass (e.g., 50 g). Next, the half decay time ( $hd$ , days) was determined using a nonlinear regression model [ $hd = \ln(1 - 0.5)/\ln(e) \times (1 / -k)$ ]. Finally, for the total decay time ( $td$ , days), we used the following equation:  $td = \ln(1 - 0.95)/\ln(e) \times (1 / -k)$  [27].

### 2.7. Data Analysis

Before the analysis, all the variables were tested for normality (e.g., by Shapiro–Wilk test) and homoscedasticity (e.g., by Bartlett test), and log transformations were applied to meet both required criteria. To find possible spatial autocorrelation, we used the Moran.I function. We did not detect any relationship between the variables and the sampling points, indicating spatial independent samples. Litter deposition, litter quality, soil properties, and litter decay rate were analyzed with two-way ANOVA. The dissimilarities between the transect sections (e.g., by Bray-Curtis' distance measure) were analyzed using a principal component analysis. It also enabled us to reduce the number of the variables to determine which variable explained most of the variation in the transect section across invaded and non-invaded environments. All analyses were run using R 3.4.0 statistical software [28].

## 3. Results

Litter deposition ( $F = 48.34$ ,  $p < 0.001$ ) varied among the studied environments and seasonal variation. In the invaded environment by *C. madagascariensis*, we found the highest significant values of litter deposition ( $4287.90 \pm 520.1$  kg ha<sup>-1</sup>) during the dry season (Figure 2).



**Figure 2.** Litter deposition (kg ha<sup>-1</sup>, mean  $\pm$  SD) in both invaded and non-invaded environments during the rainy and dry season in a tropical Cambisol, Caatinga ecoregion, Paraiba, Northeastern Brazil. Within the invaded and non-invaded environments, the same capital letters represent no significant differences, whereas within the rainy and dry season, the same small letters represent no significant differences by Bonferroni's test ( $p < 0.05$ ).



Litter N content ( $p < 0.05$ ), litter P content ( $p < 0.01$ ), litter K content ( $p < 0.05$ ), soil temperature ( $p < 0.05$ ), soil water content ( $p < 0.01$ ), and soil organic matter ( $p < 0.05$ ) varied among the studied environments and seasonal variation. In the invaded environment by *C. madagascariensis*, we found higher soil organic matter and litter N, P, and K contents when compared with the non-invaded environment. For soil temperature and soil water content, we found the highest significant values in the non-invaded environment. By considering the seasonal variation, the invaded environment had greater organic matter in the dry season, while the non-invaded environment had higher water content in the rainy season and soil temperature in the dry season (Table 3).

**Table 3.** Litter quality (N, P, and K contents,  $\text{g kg}^{-1}$ ), soil temperature, soil water content, and soil organic matter (mean  $\pm$  SD) in both invaded and non-invaded environments during the rainy and dry seasons in a tropical Cambisol, Caatinga ecoregion, Paraiba, Brazil.

Traits	Invaded		Non-Invaded	
	Rainy	Dry	Rainy	Dry
Litter N content ( $\text{g kg}^{-1}$ )	20.05 (0.47) Aa	20.25 (0.11) Aa	19.75 (0.63) Ab	19.65 (0.21) Ab
Litter P content ( $\text{g kg}^{-1}$ )	3.01 (0.03) Aa	2.9 (0.02) Aa	2.27 (0.04) Ab	2.30 (0.05) Ab
Litter K content ( $\text{g kg}^{-1}$ )	7.60 (0.04) Aa	7.64 (0.14) Aa	6.26 (0.26) Ab	6.34 (0.10) Ab
Soil temperature ( $^{\circ}\text{C}$ )	26.2 (0.85) Ab	26.5 (0.42) Ab	31.8 (0.42) Aa	32.7 (0.91) Aa
Soil water content ( $\text{g g}^{-1}$ )	12.44 (3.44) Ab	5.51 (1.73) Ba	17.66 (4.70) Aa	5.56 (4.70) Ba
Soil organic matter ( $\text{g kg}^{-1}$ )	8.45 (1.73) Ba	9.83 (1.74) Aa	4.91 (1.74) Ab	4.78 (1.41) Ab

The standard deviation is shown in parentheses. Within the invaded and non-invaded environments, the same small letters represent no significant differences, whereas within the rainy and dry season, the same capital letters represent no significant differences by Bonferroni's test ( $p < 0.05$ ).

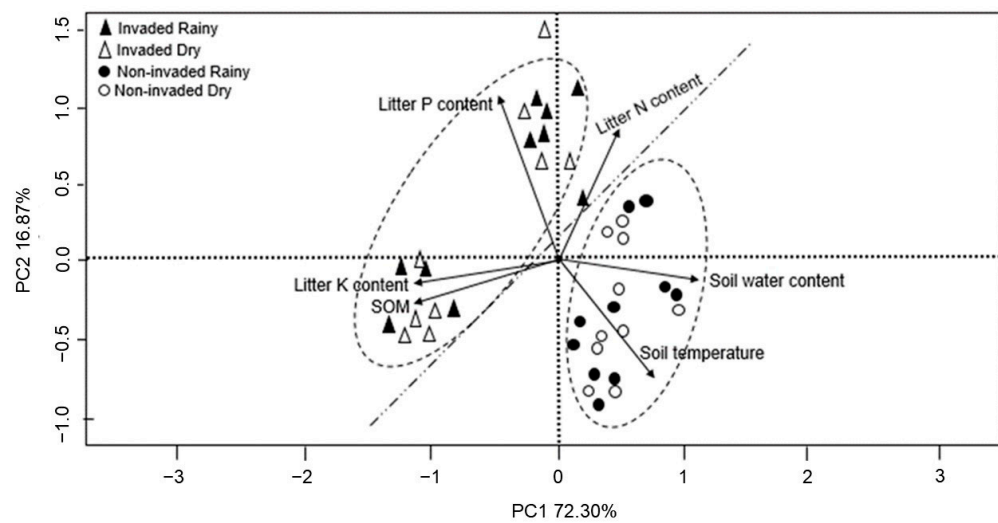
There were significant differences in the litter decay rate, half decay time, and total decay time between the invaded and non-invaded environments ( $p < 0.05$ ). For the litter decay rate, we found the highest significant values in the invaded environment, while for half and total decay, the highest significant values were found in the non-invaded one (Table 4).

**Table 4.** Litter decay rate ( $k$ ), half decay time ( $hd$ ), and total decay time ( $td$ ) in both invaded and non-invaded environments in a tropical Cambisol, Caatinga ecoregion, Paraiba, Brazil.

Studied Environments	$k$ ( $\text{Years}^{-1}$ )	$hd$ (Days)	$td$ (Days)
Invaded environment	1.10 (0.48) a	0.75 (0.39) b	3.45 (2.00) b
Non-invaded environment	0.94 (0.71) b	1.00 (0.64) a	4.37 (2.78) a

The standard deviation is shown in parentheses. Within the invaded and non-invaded environments, the same small letters represent no significant differences by Bonferroni's test ( $p < 0.05$ ).

The PCA showed that litter N, P, and K content, soil organic matter, soil temperature, and soil water content were the main factors contributing to the data variance (Figure 2). Our results showed that the studied environments were dissimilar to each other. We also found four main aspects in our PCA score plot: (i) a positive correlation between litter K content and soil organic matter in the invaded environment; (ii) a negative correlation between litter K content and litter N content; (iii) a negative correlation between soil organic matter and litter N content; and (iv) a negative correlation between soil temperature and litter P content. The two axes of the PCA explained 89.17% of data variation (Figure 3).



**Figure 3.** PCA score plot of litter quality and soil properties in the invaded and non-invaded environments during rainy and dry seasons. Triangles and points represent samples from each plot by the invaded and non-invaded environment, respectively. The two axes represent 89.17% of the data variance.

#### 4. Discussion

Our results emphasized the influence of *C. madagascariensis* on litterfall, soil organic matter, soil temperature, soil water content, and litter decomposition in a tropical Cambisol. In the invaded environment by *C. madagascariensis*, we found higher litter quality, litter decay rate, and soil organic matter than in the non-invaded environment. It enabled us to understand how *C. madagascariensis* would affect litterfall and nutrient cycling (here by considering litter quality and soil organic matter content). These results supported our hypothesis that *C. madagascariensis* can promote changes in the soil ecosystem, thus increasing resource availability and favoring the establishment of the invasive exotic plant species [3,29–31]. Essentially, this study highlighted how *C. madagascariensis* can modulate the litter deposition and quality, soil traits (temperature, soil water content, and soil organic matter), and litter decomposition in an invaded tropical Cambisol. Recent studies have demonstrated that high litterfall promoted by invasive exotic plant species changes the natural nutrient cycling process and the soil organic matter content [10,32]. Overall, *C. madagascariensis* changes the litter deposition and quality by: (i) increasing litterfall (e.g., 431.38% more litterfall than the non-invaded environment) and (ii) increasing litter quality (e.g., 1.51 to 3.05, 32.60 to 26.09, and 21.40 to 20.50% more litter N, P, and K contents (rainy to dry season) than the non-invaded environment, respectively). These results for litterfall and litter quality in the invaded environment agree with previous studies that reported litter improvements in tropical soils. Overtime the high litterfall and quality helps the invader to suppress the soil seed bank by creating a physical barrier on soil surface [3,33].

To date, the litter quality as influenced by *C. madagascariensis* has been poorly described when compared with the non-invaded environment (in our case, the Caatinga biome). *C. madagascariensis* alters litter traits of Cambisol and changes soil organic content. Our results showed that the high litter quality (characterized by low lignin content and high litter N, P, and K content) in the invaded environment may be related with: (i) extensive and deep root systems that allow the invader to access the soil nutrients more efficiently than the native plant species [34]; (ii) mutualistic associations with specialized microorganisms (e.g., arbuscular mycorrhizal fungi and bacteria) that act directly in the bioavailability of soil nutrient [4,10]; (iii) high nutrient resorption capacity (soil N, P, and K) to meet the nutritional demands of the invasive exotic plant species [35]; (iv) high abundance of litter transformers and ecosystem engineers that help the litter decomposition rate of the

invasive plant species [5]; and (v) soil food web disruption by reducing the abundance of root-feeding nematodes [3–5].

In our field study, we found a low soil temperature (6.2 °C less) on the soil surface in the invaded environment during the dry season. *C. madagascariensis* can modify soil biotic and abiotic traits by creating a physical barrier (e.g., by increasing litterfall), promoting a habitat for ants, termites, and beetles, and decreasing soil temperature, which in turn may influence soil microbial activity. This result agrees with the hypothesis of “seasonal priority effects” that reported negative changes on the soil ecosystem from a tropical ecosystem as influenced by soil temperature reduction. The changes on soil abiotic traits in the invaded environment involves an increase in litter deposition. This litter material is formed by hydrophobic leaves of *C. madagascariensis*, which create a new habitat for the soil food web in a tropical Cambisol. This high litter deposition prevents the light entry in the soil surface, and it reduces the infiltration of water by increasing the water runoff. Similar results were found by Vieira et al. [36] and Shiferaw et al. [37] in invaded areas by *Brachiaria brizantha* and *Prosopis juliflora* in the Brazilian Cerrado ecoregion, and northeastern Ethiopia, respectively.

*C. madagascariensis* increased soil fertility and nutrient cycling (soil N and P contents) in the invaded environment, particularly to a high degree of its invasion [6]. We found that litter N, P, and K contents in the invaded environment were higher than in the non-invaded environment. Not only do our results confirm that the litter quality of the invasive plant species is higher than from native plant species litter [38], but they also demonstrate that soil organic matter content differs between the invaded and non-invaded environments. In tropical conditions, other studies had reported higher litter quality from invasive litter than from native litter [29,39]. We discussed the litter quality as an important factor for litter decomposability and litter traits. According to the studies by Souza et al. [3], Lucena et al. [5], and Novoa et al. [40], invasive exotic plant species may change the soil chemical properties to their own benefit. This process is described in the “island of fertility” hypothesis [41] that defines some related aspects: (i) the invasive exotic plant species alters the soil organic matter dynamics and soil pH by increasing litterfall on the soil surface and by releasing organic acids and H<sup>+</sup> into its rhizosphere [3], (ii) the invasive exotic plant species create around its rhizosphere a nutrient-rich environment by increasing the rhizodeposition of C- and N-rich compounds, and (iii) the nutrient-rich environment improves the invasive plant species nutritional status, thus increasing the litter quality in advance. Together, these three underlining mechanisms create a favorable condition that improves the invasive litter quality and changes the soil fertility and nutrient cycling. Finally, the invasive exotic plant species may exploit positive effects of the soil microorganisms on litter decay magnitude and rate.

The highest soil organic matter contents shown in an invaded environment can be rationed with mechanisms created by invasive species in its spread process such as: (i) high rhizodeposition, invasive exotic plants species can input on its rhizosphere distinct organic compounds (e.g., organic acids, allelochemicals, and hormones), thus disrupting the soil food web structure, and altering patterns of nutrient cycling to its own benefit [42], (ii) the litter inputs the labile carbon and nitrogen compounds in the soil surface. It becomes the preferred organic material by r-strategist microorganisms [43,44], and (iii) the increase in the litter decomposition rate (as described by the k-factor) is an indicator of high decomposition activity. This high activity increases the microbial biomass, thus further contributing to the increase in soil organic matter contents [45,46].

The PCA showed that the studied environments were dissimilar considering the litter N, P, and K contents, soil organic matter, soil temperature, and soil water content. When invasive exotic plant species start colonizing resource-poor environments, they employ resource conservation traits, such as: (i) increasing soil fertility by improving the litter quality (e.g., litter N, P, and K contents); and (ii) increasing the soil organic matter content (e.g., “island of fertility” hypothesis) by improving litterfall and microbial biomass [37,47]. These two underlining mechanisms create positive plant–soil feedback to the invader that alters the entire soil ecosystem. Furthermore, the invasive plant species influences



the nutrient cycling due to litter decomposition [6,38] and the soil food web due to the physical barrier. Further, both these pathways (improved litter quality and improved litterfall) can negatively affect the soil seed bank and the natural regeneration of native plant species in the invaded environment [48]. Plant species from the non-invaded environment are extremely adapted to some conditions, such as low soil fertility, low litterfall, and high soil temperature on the soil surface. Some of these factors are also important to break down the native seed's dormancy [49–51]. To date, the invaded environment has promoted changes in litter deposition and decomposition in a tropical Cambisol. The changes promoted by *C. madagascariensis* on litter deposition can cause a disturbance in all litter factors (quality and quantity) in the invaded environment. Long-term impact on litter compartment can modify nutrient cycling differently from the observed results in the non-invaded environment [52,53]. The litter decay rate (k-factor) depends on the climate, the soil environment (e.g., soil pH, moisture, temperature, and nutrients), plant traits (e.g., lignin, C, N, and S concentrations), and decomposition activity [18,54–58]. Some factors can answer for high litter production of the invasive exotic plant species: such as (i) nutrient acquisition strategies [59]; (ii) high nutrient uptake in the system [60]; and (iii) the chemical quality of its wood or rooting depth [61]. Thus, increased litter production in invaded environments contributes to the release of the highest amount of nutrients during litter decomposition, which eventually changes the amount of nutrients, enriching the soil ecosystem in the invaded environments [62]. Therefore, the accumulation of litter produced by *C. madagascariensis* can promote a high effect on the long-term decomposition process.

The high litter quality in the invaded environment may be related to extensive and deep root systems and mutualistic associations with specialized microorganisms (e.g., arbuscular mycorrhizal fungi and bacteria) that act directly in the bioavailability of soil nutrients. Souza et al. [3] found that inoculating *C. madagascariensis*-planted soil with species of arbuscular mycorrhizal fungi (AMF) could promote more growth of *C. madagascariensis* and lead to a higher P concentration than uninoculated soil. They demonstrated that the invader might alter the composition of the AMF community in field conditions, because inoculation with this community enhanced invader growth, root colonization, and P uptake. On the contrary, a second group of microorganisms are plant–fungal pathogens. For example, two species of fungal pathogens were found to be associated with leaf spots of *C. madagascariensis*, that is *Colletotrichum gloeosporioides* and *Pseudocercospora cryptostegiae-madagascariensis* [63]. These mycological findings are of greater importance now since *C. madagascariensis* is likely to become a target for biological control agents (BCAs). A third group of microorganisms are also biocontrol agents but can indirectly influence *C. madagascariensis* by affecting plant–soil pathogens and pests. For instance, various fungi, bacteria, and entomopathogenic nematodes could act as protective BCAs against the soilborne parasites in perennial plants–cultivated soil [64,65].

## 5. Conclusions

The main finding of this study may be summarized as follows: (i) *C. madagascariensis* alters litter traits (e.g., deposition vs. decay rate) in field conditions at a tropical Cambisol; (ii) the invader changes soil organic matter content in the invaded environments; and (iii) the litter from *C. madagascariensis* showed higher litter N, P, and K contents than the litter material from *M. tenuiflora*. Increased litter production in the invaded environment determined the release of a high amount of nutrients during decomposition. These changes in the soil ecosystem may facilitate the spread of *C. madagascariensis* in Northeastern Brazil. Our findings suggest that an invaded environment by *C. madagascariensis* may present different litter traits that were created to facilitate the establishment and subsequent spread of the invader in the Brazilian northeastern territory. Despite this, our results are an important contribution on the importance of considering litter compartment, underlying how plant–soil feedback affects biological invasions. Thus, future studies should include

microbial community characterization to fully understand how soil microorganisms may decompose the invader litter material.

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