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Invasive shrub (*Lantana camara* L.) alters the tree diversity and ecosystem-level carbon pools in tropical forests of Central India

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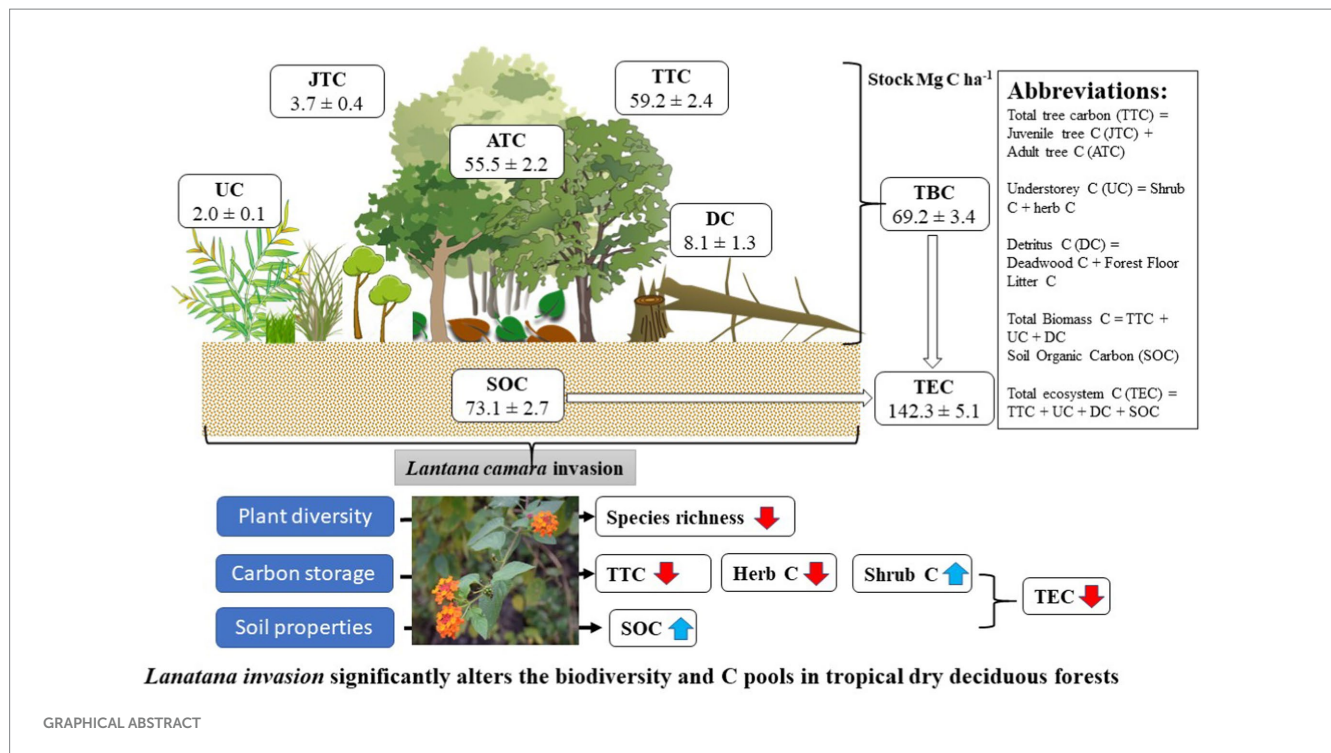
Tropical forests, known for their biodiversity and carbon (C) richness, face significant threats from biological invasions that disrupt structural and functional processes. *Lantana camara* (Family: Verbenaceae) is an invasive shrub that has spread across several Indian landscapes. The present study aimed to assess the changes in tree species richness and total ecosystem carbon (TEC) storage in *Lantana camara*-invaded (LI) and uninvaded (UI) sites in the tropical dry deciduous forests of Madhya Pradesh, India. Significantly lower species richness (SR), C storage of juveniles, total trees, and total biomass C were observed in LI sites than in UI sites. However, significantly higher C storage of shrubs + herbs (understorey), litter, and soil organic carbon (SOC) were found in LI sites than in UI sites. The percent allocation of C in tree juveniles, adults, understorey, detritus, and SOC to the TEC pool was 2.6, 39.1, 1.4, 5.5, and 51.3 in LI sites and 3.8, 49.7, 0.2, 4.0 and 42.3 in UI sites, respectively. The C stocks of tree juveniles, adults, and herbs were lower by 23.3, 15.7 and 20.3%, respectively, in LI sites than in UI sites, whereas shrub, detritus, and SOC stocks were higher by 95.1, 9.1 and 7.9%, respectively, in LI sites than in UI sites. A significant negative relationship was observed between *L. camara* density and SR, tree juvenile C, herb C, understorey C, and total ecosystem C storage, while the same had a significant positive relationship with shrub C, litter C, and SOC. The present findings revealed that the plant diversity and total C pools were altered by shrub invasion and have important implications for their quantification in these tropical forests.

KEYWORDS

shrub invasion, tree diversity, carbon pools, tropical dry deciduous forests, Central India

1 Introduction

Plant invasions alter the structural and functional diversity of ecosystems and are the major drivers of global change ecology (Ehrenfeld, 2010; Lone et al., 2019, 2022) when present in high numbers (Vilà et al., 2011). Invasive exotic species have affected the composition and structural diversity of several native ecosystems worldwide (Vitousek et al., 1996; Hughes et al., 2017). They differ from the native biota in terms of both resource acquisition and resource



consumption, which, in turn, alter ecosystem properties, disturbance regimes, and elemental cycling (Asner et al., 2010; Mandal and Joshi, 2015a). The impacts of invasion are often long-lasting, persisting in native ecosystems, even after the removal of native species (Ramaswami and Sukumar, 2016). Plant invasion is a major driver of global change, but studies on its impacts on diversity and ecosystem-level C storage in forest ecosystems are limited and fragmented (Vitousek et al., 1997; Lone et al., 2022). Some studies have suggested that plant invasion enhances ecosystem-level C storage (Stock et al., 1995; Hibbard et al., 2001), whereas few others have reported that invasion leads to a decline in diversity, ecosystem C storage, and changes in soil physio-chemical properties (Jackson et al., 2002; Gooden et al., 2009a; Kumar et al., 2020). These contrasting outcomes may result from differences in the eco-physiological traits of invasive species and the characteristics of the ecosystems they invade (Liao et al., 2007). In terrestrial ecosystems, there are predominantly six major C pools: aboveground and belowground biomass of trees, understorey vegetation, deadwood, forest floor litter, and soil (Pearson et al., 2005). Understanding the influence of plant invasion on biodiversity and each of the C pools is essential to accurately assess its impacts on C cycling (Yang et al., 2013). Invasive species affect diversity, soils, and C dynamics in several ways. They usually possess greater reproductive potential and higher competitive ability, which help to displace native species (Gooden et al., 2009a; Hughes et al., 2017). Alteration of plant communities by invasion alters the primary productivity and C sequestration potential in forests (Ehrenfeld, 2010). The C pool sizes of forests are altered by plant invasions due to variations in above- and belowground processes, which reflect on C fluxes such as rates of photosynthesis, soil respiration, etc. (Nie et al., 2017), and ultimately ecosystem-level C.

Tropical forests are biodiverse and carbon (C)-rich ecosystems and play a crucial part in the global C cycle (Dixon et al., 1994; Sullivan et al., 2017). Overall, 7–10% of the earth's area is covered by tropical forests, but they account for 34% of terrestrial primary

productivity (Beer et al., 2010). These are huge C repositories, storing about 55% of the world's forest C (471 ± 93 Pg C), and contain the highest C stocks (Pan et al., 2011). Among the different tropical forest types, dry forests are the most threatened and understudied ecosystems, and they are modulated by seasonal ecological processes. Seasonally dry forests cover 42% of tropical ecosystems and receive 250–2,100 mm of rainfall annually (Murphy and Lugo, 1986).

As per the India State of Forest Report (2019), tropical dry deciduous forests cover 40.9% of India's total forest cover. Madhya Pradesh has the largest forest cover of tropical dry forests, comprising roughly 84% of the state's forest cover. *Lantana camara* is a highly invasive plant with 650 varieties and occurs in over 60 countries (Global Invasive Species Database, 2020).

L. camara is an aggressive, fast-growing, perennial shrub of the Verbenaceae plant family. Native to tropical Central and South America, it exhibits significant genetic diversity and phenotypic plasticity, enabling it to survive under diverse climatic conditions (Adhikari et al., 2024). Initially introduced to India for ornamental purposes, it has since spread across diverse landscapes, including tropical rainforests, semi-arid regions, and mangrove ecosystems (Mungi et al., 2018). Its expansion is particularly pronounced in habitats that have experienced disturbances such as fires or floods, where native plant species are under stress. With increased canopy openings allowing light penetration and availability of soil resources, *L. camara* quickly colonizes the disturbed habitats. Seed dispersal by birds and the release of chemicals that inhibit other plants (allelopathy) give *L. camara* a competitive advantage over native species (Mungi et al., 2020). Despite long-term intensive control efforts in India, *L. camara* has only continued an upward trajectory of spread and invasion, and the spread has been projected to expand under climate change (Bhagwat et al., 2012; Adhikari et al., 2024). It covers over 13 million hectares, threatening 44% of India's forest cover by invading almost all dry deciduous forests (Sharma et al., 2005; Sharma and Raghubanshi, 2006; Goyal et al., 2018; Mungi et al., 2020). *L. camara*

has also extensively invaded Central India's forest ecosystems (Love et al., 2009; Bhagwat et al., 2012; Wagh and Jain, 2018). The main goal of this research was to understand the effects of shrub (*L. camara*) invasion on plant species richness and C pools {trees, understorey, detritus (deadwood + forest floor litter), and soil organic carbon} of Central Indian tropical dry deciduous forests. Our specific objectives were: (1) to assess the impacts of *L. camara* invasion on plant diversity and ecosystem-level C pools and (2) quantify changes in these parameters due to shrub invasion.

2 Materials and methods

2.1 Study area

The present study was undertaken in three forest study sites in Sagar, Madhya Pradesh, Central India (Figure 1; Table 1). The study area is located in north-central Madhya Pradesh and is surrounded by the Vindhya mountain range. The forest type in the study region belongs to group 4b as per Champion and Seth's (1968) classification. A subtropical climate with a hot summer (March to mid-June),

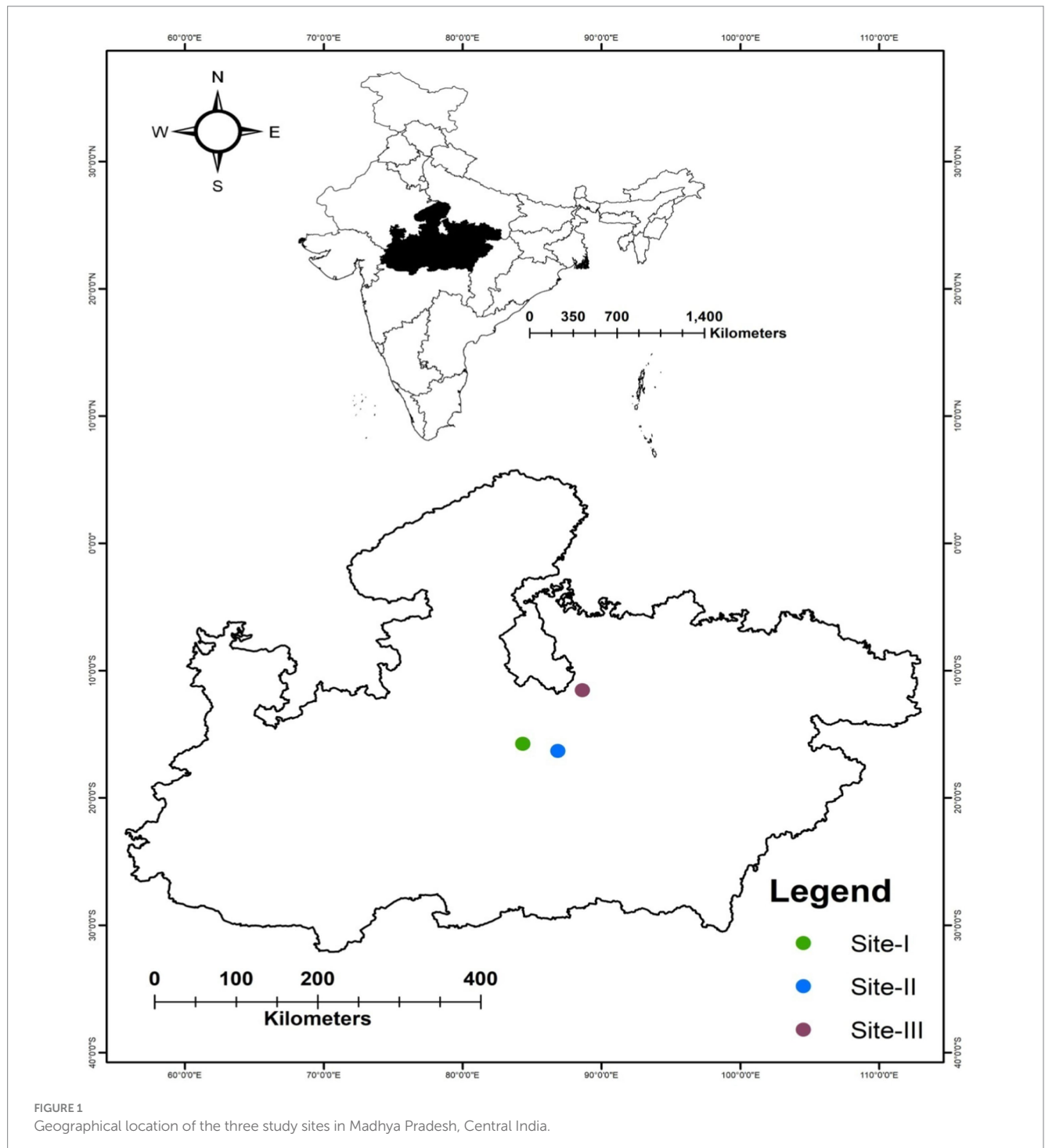


TABLE 1 Study site characteristics of uninvaded (UI) and *Lantana*-invaded (LI) sites of tropical dry deciduous forests in Madhya Pradesh, Central India.

Parameter	Uninvaded (UI)			<i>Lantana</i> -invaded (LI)		
	Site-I	Site-II	Site-III	Site-I	Site-II	Site-III
Latitude (°)	23.46–23.47	23.19–23.20	24.39–24.39	23.46–23.47	23.19–23.20	24.39–24.39
Longitude (°)	78.77–78.78	79.03–79.04	79.23–79.23	78.77–78.78	79.03–79.04	79.23–79.23
Altitude (m)	536–568	428–476	386–397	535–588	435–460	378–393
Mean annual temperature (°C)	25.2	25.2	24.8	24.7	25.1	25.2
Mean annual precipitation (mm)	1,185	1259.2	1122.8	1189.8	1,247	1126.4
Tree density (No. ha ⁻¹)	528	443	400	343	354	300
Tree basal area (m ² ha ⁻¹)	22.5	18.2	18.3	15.2	12.3	16.5
Tree species richness	21	30	17	13	24	17
Genera	20	29	16	12	22	17
Families	13	17	11	8	13	12
Mean tree DBH	20.96	19.8	22.2	21.4	19.3	23.3

followed by a rainy season (mid-June to September) and a cool winter (October to February), prevails in the study region. The mean annual minimum temperature is 11.6°C, and the mean maximum temperature is 40.7°C, whereas the mean annual rainfall is 1197.6 mm in the study area (WorldClim, 2024). The southwestern region of the district receives the heaviest rainfall, and the intensity decreases toward the north and east. The soil type is clayey to sandy loam in all the study sites. All three study sites are comprised of open forests, with grazing, firewood, and non-timber forest produce collected by local people being observed. *Butea monosperma*, *Tectona grandis*, *Lagerstroemia parviflora*, and *Diospyros melanoxylon* are the most prevalent tree species in this forest, which has now been invaded by *L. camara* (Dar et al., 2019).

2.2 Sampling of diversity and biomass

Fieldwork was carried out in 2017 and 2018, and three study sites were chosen after an extensive reconnaissance survey (Supplementary Figure 2). The study sites were chosen based on the differences in altitude, structure, and composition (Table 1; Supplementary Tables 1–3). Each site was divided into two sub-sites based on the presence or absence of the shrub, *L. camara* – they were classified as uninvaded (UI; *L. camara* cover absent) and *L. camara*-invaded (LI; presence of *L. camara* cover >50%) following Gooden et al. (2009a). In each sub-site, 10 plots of 2,500 m² (50 m × 50 m) were laid randomly in the study site (a total of 60 plots – 30 in UI and 30 in LI). The study plots were randomized based on a rarefaction curve analysis to ensure representative sampling (Figure 2).

Phytosociological attributes such as tree richness, frequency, density, basal area, and size class distribution were enumerated in all the plots. Each 2,500 m² plot was further partitioned into 25 (100 m²) quadrats for easy sampling (Misra, 1968). The stems were considered as trees: >3–9.9 cm DBH (juveniles) and ≥ 10 cm DBH (adults) (Chaturvedi et al., 2012a; Chaturvedi et al., 2012b; Baboo et al., 2017). Tree and liana stem with a diameter greater than 3 cm at breast height (DBH) were measured (Knight, 1963). The girths of the

multi-stemmed trees were measured separately. The above- and belowground (AGB and BGB, respectively) C storage was estimated following the standard biomass equations using tree DBH, height, and wood density (Zanne et al., 2009). The height of all trees was measured using a digital Haglof clinometer.

Allometric equations used:

The tree AGB was estimated following Chave et al. (2014):

$$AGB = 0.0673 \times (\rho \times DBH^2 \times H) 0.976$$

The AGB of tree juveniles was calculated following Chaturvedi et al. (2012a), Chaturvedi et al. (2012b):

$$AGB = 3.344 + \left(0.443 \times \left(\ln \left((DBH)^2 \right) \right) \right)$$

The woody climber biomass was estimated following Schnitzer et al. (2006):

$$AGB = \text{EXP} \left(-1.484 + 2.657 \times (\ln(DBH)) \right)$$

Tree BGB was calculated following Cairns et al. (1997):

$$BGB = \text{EXP} \left(-1.0587 + 0.8836 \times (\ln(AGB)) \right)$$

The BGB of tree juveniles and climbers was estimated following Ravindranath and Ostwald (2008):

$$BGB = AGB \times 0.26$$

2.3 Sampling understorey and detritus

To sample the understorey, ten 25 m² (5 m × 5 m) quadrats were laid in each plot to record shrubs (including *L. camara*) and climbers. An additional ten 1 m² (1 m × 1 m) quadrats were used for herbs. The understorey vegetation was clipped at the base during the peak growing period. The clipped biomass was weighed fresh on-site with a digital balance in the field, and five replicate samples were transferred

to the lab. These samples were dried in a hot-air oven at $105 \pm 5^\circ\text{C}$ for 72 h and were weighed again for dry mass. The detritus biomass (deadwood + litter) was calculated following Ravindranath and Ostwald (2008). The estimated biomass was converted to C by following the conversion factor (0.5) as per the Intergovernmental Panel on Climate Change (IPCC, 2006).

2.4 Soil sampling and laboratory analyses

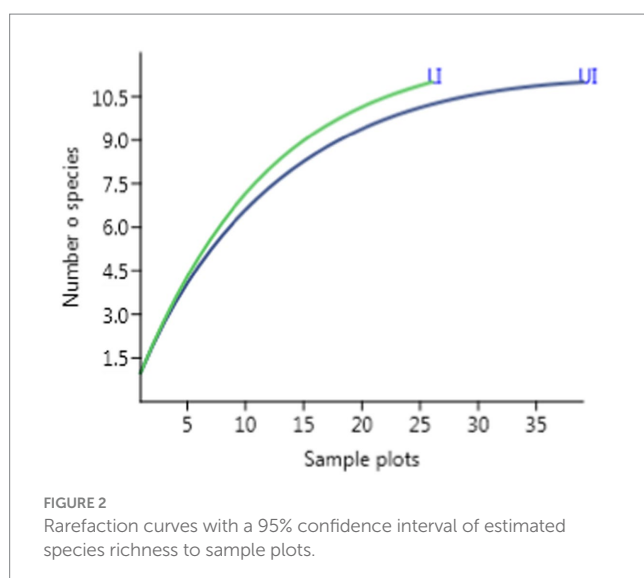
The soil samples in the LI and UI subsites were collected in all the plots. Five random points were chosen in each plot, and standing crop litter was cleared before collecting the soil samples. A soil core sampler with an internal diameter of 6 cm and a total of 60 soil samples (at a depth of 0–50 cm) were collected in labeled polyethylene bags before being transported to the laboratory. The samples were air-dried, sieved, and ground to a fine powder in the laboratory.

Walkley and Black's (1934) method was used to estimate soil organic carbon (SOC). For bulk density (BD; g/cm^3) estimation, three replicates of undisturbed soil cores (0–50 cm) were collected in each plot. The soil samples were taken to the laboratory, oven-dried at $105 \pm 5^\circ\text{C}$ for 72 h, and then re-weighed. The coarse rocky fragments were removed using a 2 mm sieve and re-weighed. Soil BD was calculated following Pearson et al. (2005):

$$\text{Bulk density } (\text{g} / \text{cm}^3) = \frac{\text{Oven dried mass } (\text{g} / \text{m}^3)}{\text{Core cylinder volume } (\text{m}^3) - \text{Mass of coarse fragments } (\text{g}) / 2.65 (\text{g} / \text{cm}^3)}$$

The SOC of soil samples was calculated following Pearson et al. (2005).

$$\text{SOC } (\text{Mg C ha}^{-1}) = \left[\left(\text{BD } (\text{g} / \text{m}^3) \times \text{Depth } (\text{cm}) \times \text{C} \right) \right] \times 100$$



Soil moisture (M%) was measured using the gravimetric method, while soil pH (1:2.5 ratio of soil to water) was determined using a digital pH meter. Climatic variables, such as minimum and maximum temperatures, mean annual temperature (MAT), and mean annual precipitation (MAP), were obtained for all plots from the WorldClim dataset (WorldClim, 2024) using the *sp.* and *raster* packages in R 3.6.2. Additionally, topographic variables, such as slope and aspect, were derived using R 3.6.2.

2.5 Statistical analyses

Ecosystem-level carbon storage was calculated by summing carbon stored in trees, the understory, detritus, and soil organic carbon (SOC) (Ravindranath and Ostwald, 2008; Kothandaraman et al., 2020). A one-way analysis of variance (ANOVA) was used for statistical analysis. Tukey's HSD test tested the differences in mean \pm standard error of diversity, vegetation C stocks, and SOC ($p < 0.05$). All the statistical analyses were conducted using SPSS 22.0 (SPSS Inc, 2013). Linear correlations were conducted to assess the relationships of *L. camara* density with other descriptor variables (Supplementary Table 5).

3 Results

3.1 Impact of *L. camara* on richness and species diversity

Significantly lower ($p < 0.05$) species richness (SR, 98 species) was observed in LI sites than in UI sites (132 species). The mean SR of trees was significantly ($p < 0.05$) lower in LI sites (saplings - 13, juveniles - 30, and adult trees - 29) than in the UI sites (saplings - 21, juveniles - 33, and adult trees - 40). For saplings, juveniles, and adults, the total SR was 55, 72, and 54 in LI, and 71, 98, and 76 in UI sites, respectively (Figure 3; Supplementary Table 1; Supplementary Figures 5–9).

3.2 Carbon stocks of trees, understory and detritus

The mean aboveground total tree C stock (juvenile carbon + adult carbon) was significantly ($p = 0.032$) lower in LI sites ($48.1 \pm 3.6 \text{ Mg C ha}^{-1}$) than in UI sites ($66.7 \pm 4.8 \text{ Mg C ha}^{-1}$; Figure 4). The total tree aboveground C ranged from 43.1 to 50.6 Mg C ha^{-1} in LI sites and 59.4 to 72.2 Mg C ha^{-1} in UI sites. The belowground C stock also showed the same trend as the latter, which has been calculated from the former. Significantly ($p < 0.001$), higher mean shrub C stock was observed in LI sites ($1.87 \pm 0.13 \text{ Mg C ha}^{-1}$) than in UI sites ($0.008 \pm 0.004 \text{ Mg C ha}^{-1}$) sites. Overall, significantly ($p < 0.001$) higher total understory C stock (shrub C + herb C) was observed in LI sites than in UI sites. The total understory C ranged from 1.7 to 2.4 Mg C ha^{-1} in LI sites and from 0.08 to 0.41 Mg C ha^{-1} in UI sites.

The mean litter C stock was significantly ($p < 0.0001$) higher in LI sites ($1.8 \pm 0.1 \text{ Mg C ha}^{-1}$) than in UI sites ($1.5 \pm 0.1 \text{ Mg C ha}^{-1}$). Overall, the mean detritus C stock (litter carbon + deadwood carbon)

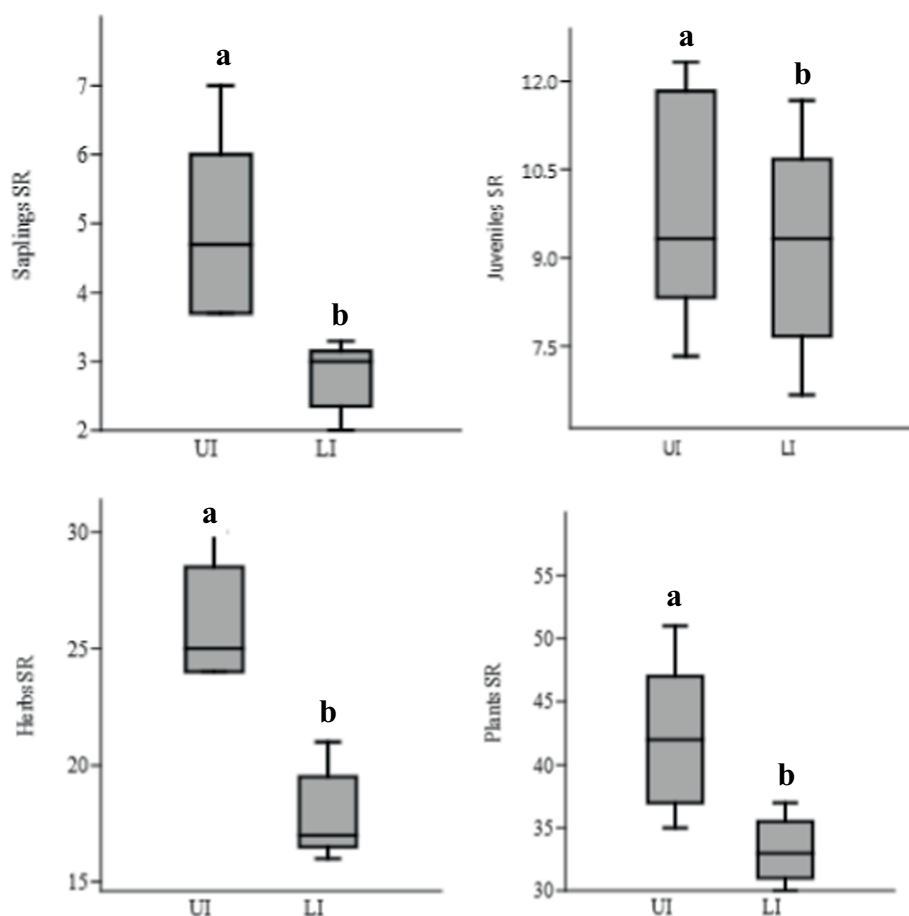


FIGURE 3

Species richness (SR; No. of species) of tree saplings, juveniles, herbs, and total plants (trees, herbs, and shrubs) in unininvaded (UI) and *Lantana*-invaded (LI) sub-sites. Different letters show ($p < 0.05$) different means significantly between them by Tukey's HSD *post hoc* test.

was higher in LI sites ($8.1 \pm 1.3 \text{ Mg C ha}^{-1}$) than in UI sites ($6.2 \pm 0.7 \text{ Mg C ha}^{-1}$), although non-significant. The mean total biomass C stock of all the pools (tree C + understorey C + detritus C) was found to be significantly ($p < 0.05$) lower ($69.2 \pm 3.4 \text{ Mg C ha}^{-1}$) in LI sites than in UI sites ($88.5 \pm 5.9 \text{ Mg C ha}^{-1}$; [Figure 4](#); [Supplementary Table 4](#)).

3.3 Soil organic carbon (0–50 cm)

SOC stocks were significantly ($F = 10.67$, $p < 0.001$) higher in LI sites than in UI sites. In LI sites, SOC stocks ranged from 64.6 to 84.1 Mg C ha^{-1} , with a mean of $73.1 \pm 2.7 \text{ Mg C ha}^{-1}$, whereas, in UI sites, the SOC stocks ranged from 55.7 to 76.1 Mg C ha^{-1} , with the mean of $65.2 \pm 2.8 \text{ Mg C ha}^{-1}$ for a depth of 0–50 cm ([Supplementary Table 4](#)). *L. camara* density was related to changes in soil properties. The values of BD (g cm^{-3}) and pH were significantly ($F = 12.96$, $p < 0.05$) lower in LI sites than in UI sites, whereas moisture (M%) was significantly ($F = 68.55$, $p < 0.001$) higher in LI sites than in UI sites. The SOC and soil total nitrogen (STN) stocks were significantly ($F = 48.3$, $p < 0.001$; $F = 51.7$, $p < 0.001$) higher in LI sites than in UI sites ([Figure 5](#)).

3.4 Ecosystem-level carbon storage

The total ecosystem C (TEC) storage, comprising tree juveniles, adults, understorey (shrubs + herbs), detritus (litter + deadwood), and SOC, varied significantly ($p < 0.001$) among LI sites and UI sites ([Supplementary Table 4](#)). Significantly ($p < 0.05$) lower TEC pool was found in LI sites (mean $142.4 \text{ Mg C ha}^{-1}$) than in UI sites (mean $153.7 \text{ Mg C ha}^{-1}$).

3.5 Carbon allocation patterns

The C allocation pattern among the different ecosystem components was markedly different in LI sites from those of UI sites. Overall, tree juveniles, adults, understorey, detritus, and SOC contribute 3.7, 55.5, 2.0, 8.0, and 73.1 Mg C ha^{-1} , and 5.9, 76.1, 0.21, 6.27, and 65.3 Mg C ha^{-1} in LI sites and UI sites, respectively ([Supplementary Table 4](#)). The percent allocation of tree juveniles, adults, understorey, detritus, and SOC to the total ecosystem C pool was 2.6, 39.1, 1.4, 5.5 and 51.3% in LI sites and 3.8, 49.7, 0.2, 4.0 and 42.3% in UI sites, respectively ([Figure 6](#)). In LI sites, carbon stocks of tree juveniles, adults, and herbs were reduced by 23.3, 15.7, and 20.3%, respectively, compared to UI

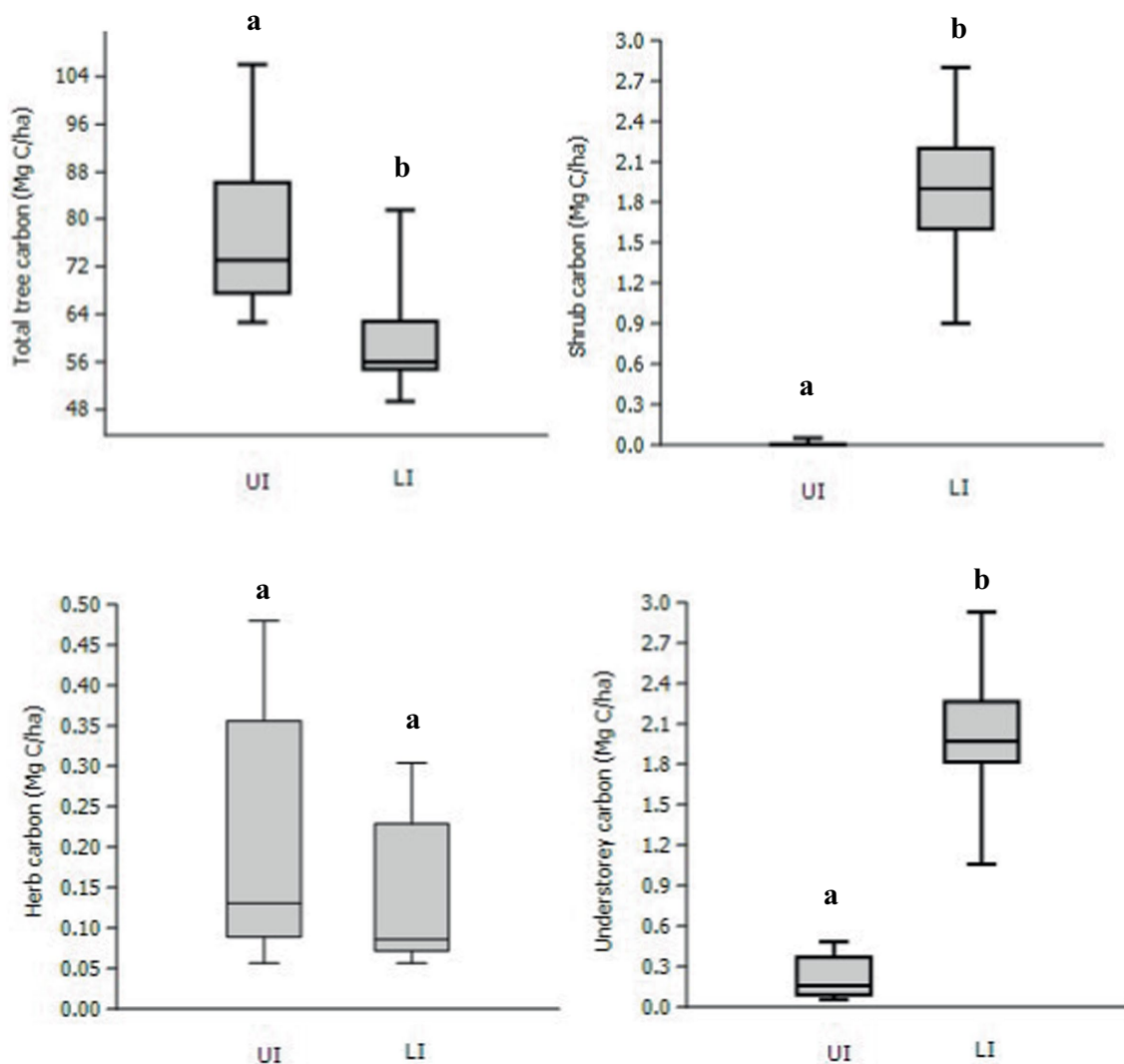


FIGURE 4 (CONTINUED)

sites. Conversely, shrub, detritus, and SOC stocks increased by 95.1, 9.1, and 7.9%, respectively (Supplementary Figures 1,4).

3.6 Diameter class-wise distribution and percent change in carbon stock

In all three LI sites, the 20.1–30 cm diameter class held the highest carbon stock, followed by the 30.1–40 cm diameter class (Figure 7A). The C stocks were low by 35, 23.7, 23, and 21.8% in the 60.1–70, >80.1, 0–10, and 30.1–4–40 cm diameter classes, respectively, in LI sites than UI sites (Figure 7B).

3.7 Relationships of *L. camara* density with descriptor variables

A significantly negative relationship has been found between *L. camara* density and plant diversity ($r = -0.459$), tree juvenile C ($r = -0.475$), herb C ($r = -0.384$), understorey C ($r = -0.686$), and

total ecosystem C storage ($r = -0.208$). On the other hand, a significant positive relationship was observed with shrub C ($r = 0.645$), litter C ($r = 0.425$), and SOC ($r = 0.89$; Table 2). The SOC, STN, and M% showed significant positive correlations, whereas soil pH correlated significantly negatively with *L. camara* density. Soil bulk density had a non-significant negative relationship with *L. camara* density.

The Principal Components Analysis (PCA) assessed the relationships among diversity, structural attributes, and environmental factors with *L. camara* density (Supplementary Figure 3). Eigenvalues of the dominant axis were 6.25, 4.92, 3.93, 2.03, and 1.04, respectively, and the corresponding percentage variances were 28.4, 22.4, 17.9, 9.2, and 5.8. These values reflect variations in elevation, mean annual precipitation, slope, moisture, and pH, which accounted for 83.7% of the variation in *L. camara* density.

4 Discussion

Biological invaders represent a major change element in forest ecosystems (Vitousek et al., 1996). They are known for their impacts

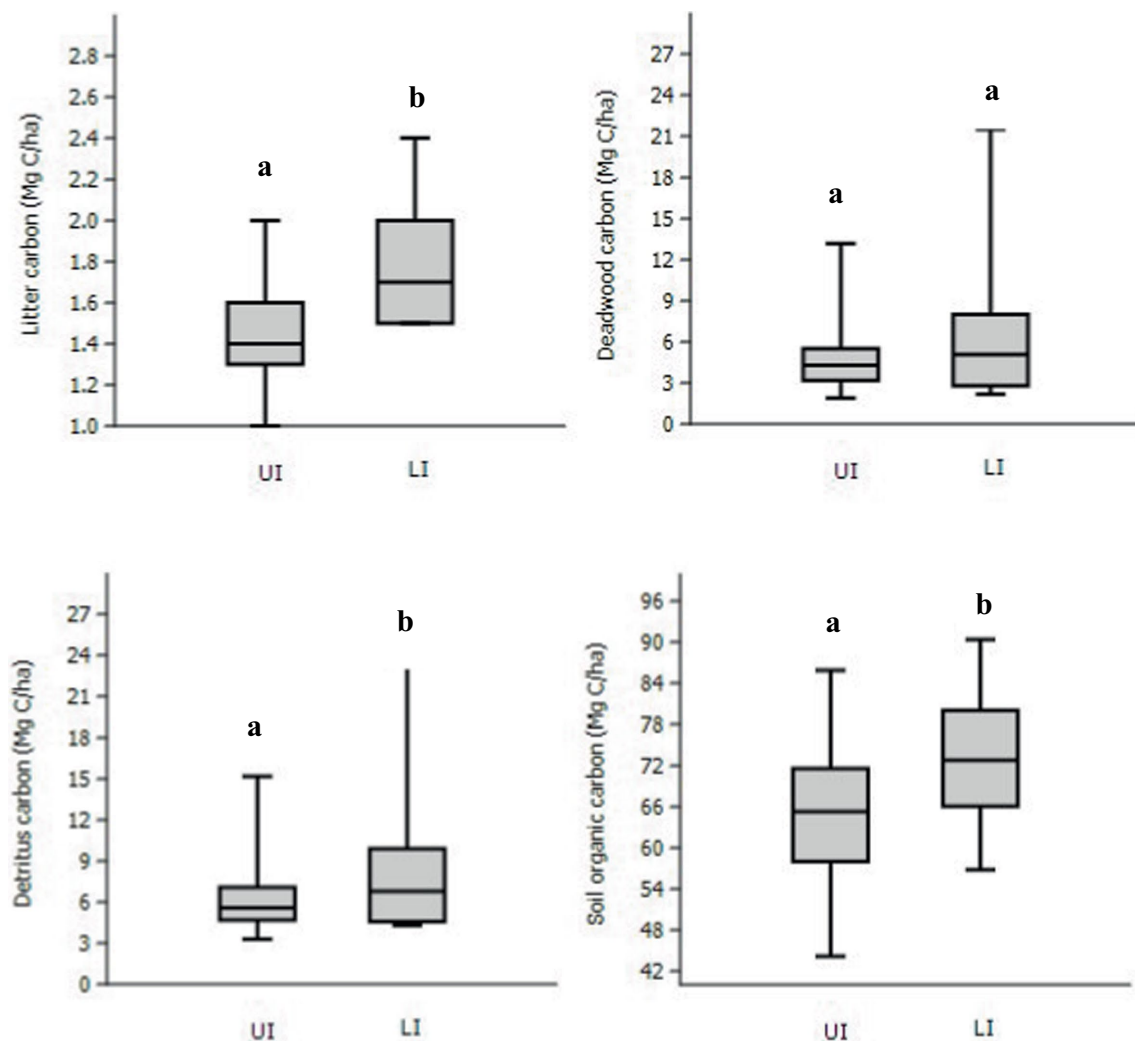


FIGURE 4

Variation in carbon stocks (total tree C, shrub+herb+understorey C, litter+deadwood+detritus C, SOC) in uninvaded (UI) and *Lantana*-invaded (LI) sub-sites. Different letters show ($p < 0.05$) different means significantly between them by Tukey's HSD post hoc test.

on the community structure, species composition, and diversity of both above- and belowground communities, with significant changes in functioning and processes (Gaertner et al., 2009; Ehrenfeld, 2010; Vilà et al., 2011; Richardson et al., 2011; Gioria et al., 2014). The C stocks of different pools are greatly impacted by shrub invasion by changing their structure, above- and belowground biomass, litter production, and SOC (Tilman et al., 2001; Liao et al., 2008a, b; Fornara and Tilman, 2008). *L. camara* is a widely distributed invasive weed and has engulfed the maximum area of tropical dry forests in the Central Indian landscape (Mungi et al., 2020). Thus, the invasion could drastically alter the structural and functional processes. Any such change by invasion would significantly influence regional and global C cycling, exacerbating the effects of climate change.

The total carbon stocks of adult trees (above- and belowground) were 15.4% lower in LI than in UI sites, though this difference was not statistically significant ($p = 0.060$). This insignificance in total adult tree biomass C could be attributed to the predominance of *Tectona grandis* trees with almost similar densities, basal areas, and representation in higher diameter classes (≥ 60 cm DBH). Similar

results were obtained by Litton et al. (2006), who reported insignificantly higher aboveground tree biomass stocks between native and *Pennisetum setaceum*-invaded tropical dry deciduous forests in Hawaii, and Gaudel et al. (2016), who reported lower aboveground tree biomass and C stocks in areas that are highly invaded by *Mikania micrantha* compared to medium- and lowly invaded areas in Parsa Wildlife Reserve, Nepal.

In the present study, biomass C stocks of juvenile trees were significantly ($p < 0.0001$) lower by 22.9% in LI sites than in UI sites (Supplementary Table 4). Our results confirm with Litton et al. (2006) and Gaudel et al. (2016), who reported significantly lower biomass C stocks in tree seedlings in areas invaded by *Pennisetum setaceum* and *Mikania micrantha*, respectively. This significant difference in juvenile tree biomass and C stock may be due to the presence of greater *L. camara* density/cover, which was above the threshold limit ($> 70\%$ cover) in these sites (Gooden et al., 2009a), which could have impacted the growth of tree saplings and juveniles, thereby reducing their density and basal area. Plant invasion can result in changes in the structure, composition, diversity, evenness, and regeneration potential of forests

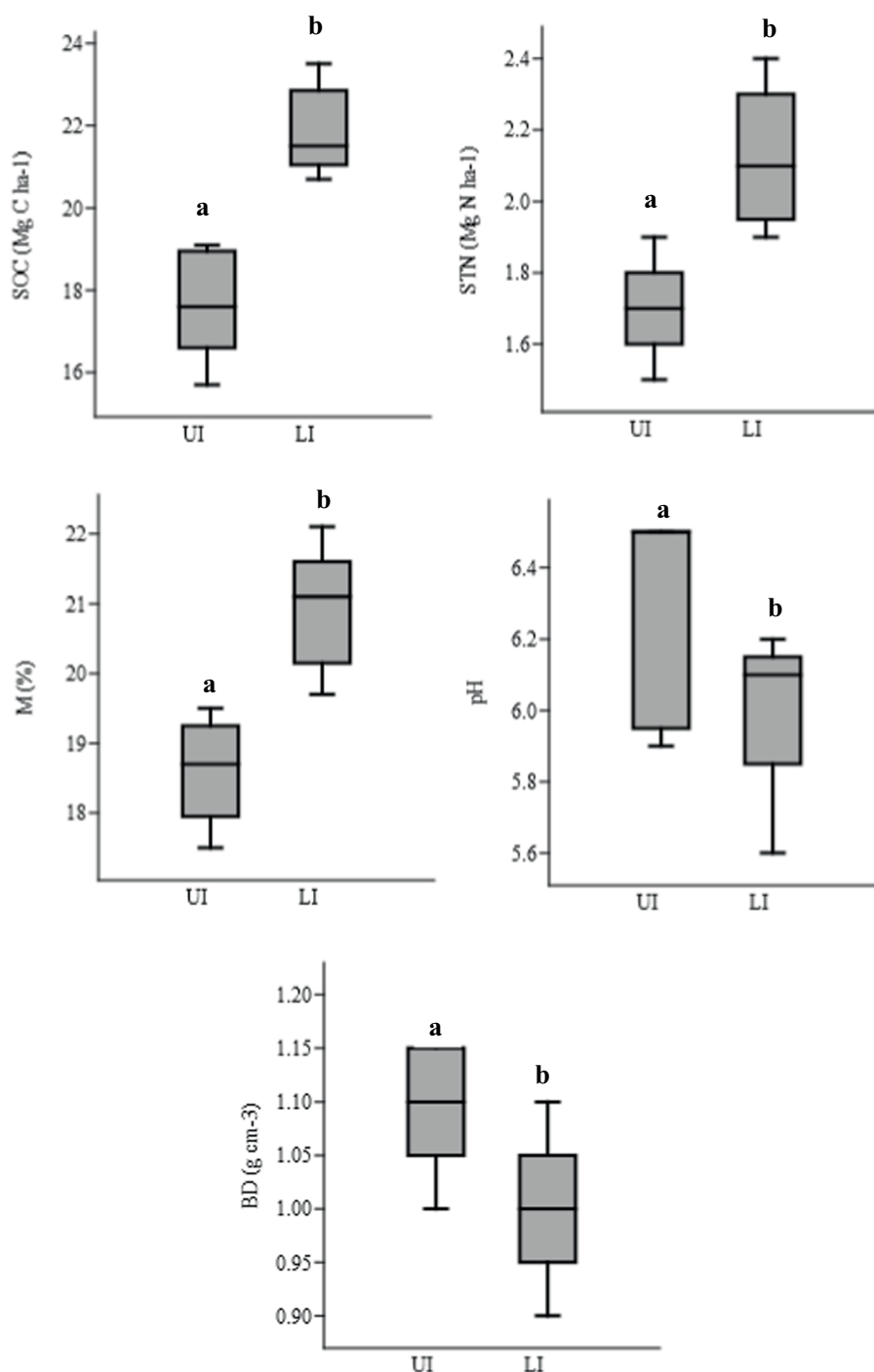


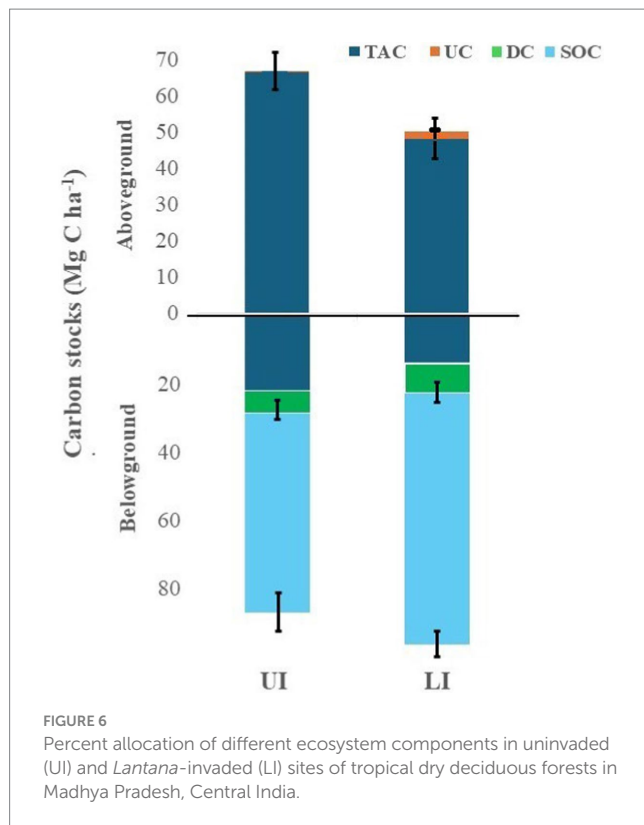
FIGURE 5

Soil organic carbon (SOC; Mg C ha⁻¹), soil total nitrogen (STN; Mg C ha⁻¹), moisture (M; %), pH, and bulk density (BD; g cm⁻³) in uninvaded (UI) and *Lantana*-invaded (LI) sites. Data are presented as mean values. Different letters show significant differences at a p -value of <0.05.

(Saxena and Singh, 1985; Saxena, 1991; Ambika et al., 2003; Taylor et al., 2012; Kumar et al., 2020). The higher density of *L. camara* alters the structure, species composition, diversity, and biomass of native plants. The impacts of invasion by woody plants on native tree juvenile and adult biomass C stocks are reported to be greater than those of non-woody and non-nitrogen-fixing plants (Liao et al., 2008b).

Total tree biomass and carbon stocks were significantly lower (by 17.5%; $p < 0.05$) in LI sites compared to UI sites. Invasion could

exert positive, negative, or neutral impacts on different C pools, depending on the type of invader and its characteristics and the type of community undergoing invasion (Hughes et al., 2017). In the present study, the lower total tree biomass and C stocks in LI sites than UI sites are due to the lower tree densities and basal areas in LI sites. The invasion of *L. camara* has altered the structural diversity, changing the size of saplings and juveniles and their relative dominance (Ens and French, 2008; Fisher et al., 2009).



Invasive plants impact native plants by changing their structural composition (Mason and French, 2008). Hejda et al. (2009) reported a reduction in structural diversity in invaded plots compared to the uninvaded plots. High *L. camara* invasion suppresses the growth and recruitment of vegetation by changing the microenvironment and inhibits germination by the release of allelochemicals in soil (Gentle and Duggin, 1997; Lewis et al., 2004). *L. camara* thickets impede the recruitment of smaller individuals by outcompeting them for essential resources, including light and space (Gooden et al., 2009b; Ramaswami and Sukumar, 2011, 2016; Sundaram and Hiremath, 2012). This reduces basal area, which is an indicator of biomass C (Litton et al., 2006; Adomako et al., 2019; Raha et al., 2020).

The shrub C stock was significantly more at 95.1% in LI sites than in UI sites, whereas the herbaceous C stock was significantly less at 23.2% in LI sites than in UI sites. The significantly ($p < 0.0001$) higher C stocks of shrubs in LI sites are due to the presence of higher density, basal area, and biomass of *L. camara* in these sites than in the UI sites. However, *Lantana* density did not significantly correlate with shrub biomass, excluding *L. camara* ($R^2 = 0.10$). Our values of shrub biomass and C stocks are in concurrence with the findings reported by Mandal and Joshi (2015b) in the subtropical deciduous forests of western Himalaya, India (3.82 Mg C ha⁻¹), Pande (2005) from tropical dry deciduous teak forests (0.69–3.77 Mg ha⁻¹), Oraon (2012) in tropical dry deciduous forests, Chhattisgarh (1.15 and 6.79 Mg ha⁻¹), Jhariya et al. (2014) in the tropics of Chhattisgarh, India (2.48–5.88 Mg ha⁻¹), but lower than the values reported by Jhariya (2017) from Boramdeo Wildlife Sanctuary, Chhattisgarh, India (6.82–15.71 and 2.93–6.76 Mg ha⁻¹ biomass and C, respectively), Singh and Singh (1991) from tropical dry forest of Vindhyan region (7.1 and 20.98 Mg ha⁻¹) and Swamy et al. (2010) from tropical evergreen forests of Western

Ghats (38.1–86.3 Mg ha⁻¹). The significantly ($p < 0.0001$) lower C stock of herbs in LI sites could be due to the lower herb density, basal cover, and evenness. *L. camara* canopies are known to intercept the incoming sunlight, causing shade (Asner et al., 2008, 2010), inhibiting the recruitment of understory herbaceous vegetation by displacing them through competition for resources (water, nutrients, light, space, etc.), allelopathy and by altering soil properties (Walck et al., 1999; Vila and Weiner, 2004; Yurkonis et al., 2005; Bjerknes et al., 2007; Pejchar and Mooney, 2009; Timsina et al., 2011). Similarly, Hughes et al. (2006) have also reported a decline in herbaceous C pool due to *Prosopis glandulosa* encroachment in the Southern Great Plains of the United States.

Significantly ($p < 0.001$), higher litter and deadwood C stocks (non-significant) were recorded in LI sites than in UI sites. Litter and deadwood C were higher by 9.1 and 14.5%, respectively, in LI sites. The higher litter C stocks in LI sites are due to a large accumulation of *L. camara* litter and non-extraction of deadwood timber by the local people and the forest department. *L. camara* thickets also hinder entering the forest for timber extraction. High *L. camara* density might be the reason for higher detritus biomass and C stocks in LI sites than in UI sites because the latter are relatively open and have less surface litter.

More SOC stocks in LI sites than in the UI sites could have been due to significantly higher litter inputs with varying litter composition, higher nitrogen concentration, higher moisture content, and lower lignin and cellulose content that might have enabled rapid decomposition of *L. camara* litter (Ehrenfeld, 2003; Liao et al., 2008a; Li et al., 2016). This implies that the litter quantity and quality may alter soil nutrients.

The TEC stocks and allocation patterns showed significant changes between LI sites and UI sites. Invasion by woody plants tends to have considerable impacts on C stocks and profoundly alters the allocation patterns (Liao et al., 2008a). In this study, the greater allocation of C stocks in shrubs, detritus, and soil is due to higher *L. camara* density, non-extraction of deadwood, and greater litter inputs, which may have resulted in higher allocation in these components. On the other hand, lower allocation of C stocks in tree juveniles, adults, and herbs could be because high *L. camara* density could have inhibited their growth and recruitment by intercepting light, releasing allelochemicals, resource competition, and so on, as suggested by Asner et al. (2010).

In the present study, SOC showed significant positive correlations with *L. camara* density, basal area, biomass, and litter. Similarly, Sharma and Raghubanshi (2006, 2007) have found a positive relationship between *L. camara* cover and SOC in tropical dry deciduous forests in India. Mandal and Joshi (2014, 2015b) have found a strong relationship between *L. camara* biomass and SOC in the central Himalayas, India. Gómez-Rey et al. (2013) have also found a positive relationship between shrub density and soil organic matter in Mediterranean oak woodland.

The distribution of different size classes indicates the C storage and regeneration potential of any forest landscape. Small, medium-sized, and large trees are important in C storage in any forest ecosystem (Brown et al., 1997; Baishya et al., 2009; Borah et al., 2013). In the present study, C stocks were reduced in most of the diameter classes in LI sites. This could be due to lower density and basal area in the invaded sites. *L. camara* impedes the recruitment of small-sized tree individuals into larger diameter classes and the growth of large

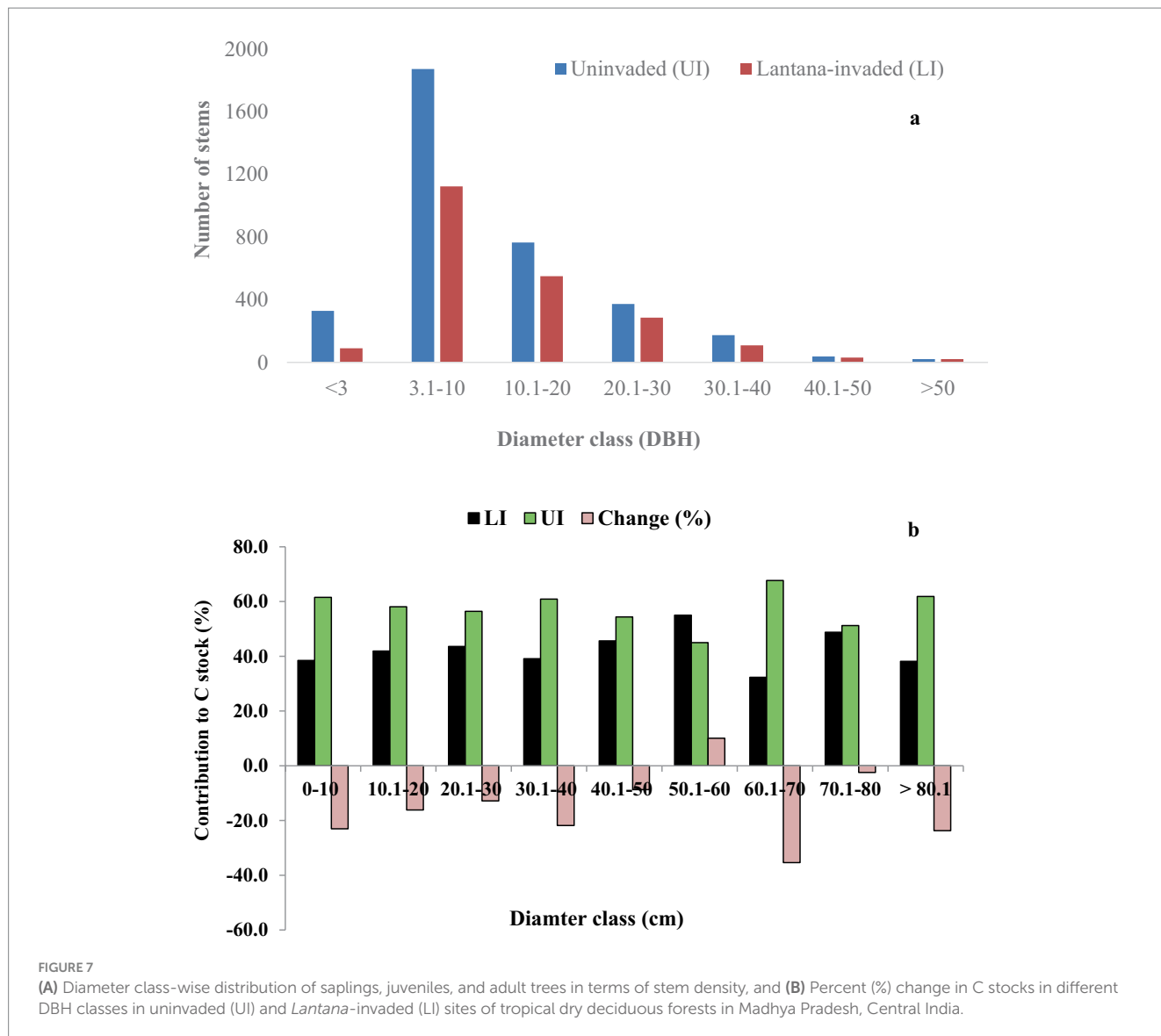


FIGURE 7 (A) Diameter class-wise distribution of saplings, juveniles, and adult trees in terms of stem density, and (B) Percent (%) change in C stocks in different DBH classes in uninvasive (UI) and *Lantana*-invaded (LI) sites of tropical dry deciduous forests in Madhya Pradesh, Central India.

TABLE 2 Correlations (*r*-values) between *Lantana* density and other descriptor variables.

Descriptor	<i>r</i> -value	Descriptor	<i>r</i> -value
Tree juvenile C	-0.475*	SOC (0–50 cm)	0.890*
Tree adult C	-0.116	Total ecosystem C	-0.208*
Total tree C	-0.293	Diversity	
Shrub C	0.645*	Tree saplings	-0.720*
Herb C	-0.384*	Tree juveniles	-0.280
Understorey C	-0.686*	Tree adults	-0.261
Litter C	0.425*	Total trees	-0.110
Deadwood C	0.394	Herbs	-0.385
Detritus C	0.413		

r-values with an asterisk represent a significant ($p < 0.05$) relationship between the variables after Bonferroni correction. Tree C includes both above- and below-ground C stock.

DBH classes, causing a reduction in density and basal area (Alemu and Terefe, 2015). The conversion of these forests to shrublands will reduce the tree C pools (Jaramillo et al., 2003; Bonino, 2006).

Mitigating the spread of *L. camara* using fire and biological control has been recorded as early as 1921 in India (Troupe, 1921; Bhagwat et al., 2012). However, fire is known to facilitate further expansion of this invasive shrub (Hiremath and Sundaram, 2005). However, chemical control followed by planting fast-growing native species has yielded positive results in Punjab, India (Luna et al., 2009). There have also been efforts to contain *L. camara* spread while boosting economic benefits by using it as a green compost and using the stems to make baskets (Nanjappa et al., 2005; Sharma et al., 2005). Love et al. (2009) developed a new strategy to manage *L. camara* invasion in Indian forest ecosystems, which is to first remove the *L. camara* plants by cutting rootstock method followed by weeding of its saplings under the trees (to prevent further seed dispersal) and ecological restoration of grasslands/forests as per the stakeholder needs. Cost-benefit analyses of different management options need to be considered while devising the appropriate control plan (Negi et al., 2019). Successful management of *L. camara* invasion required an integrated approach involving all stakeholders, including state governments, national networks, and, where necessary, global coordination (Adhikari et al., 2024).

The invasion of *L. camara* in tropical dry deciduous forests significantly alters diversity, biomass, and C pools, as well as their allocation patterns, in Central Indian forests. However, it is important to note that this study is based on a one-time survey, meaning that the invaded sites may have had lower diversity and carbon levels even before the invasion. However, efforts were made to ensure that the study design adequately captured the differences between uninvaded and invaded sites. For example, the UI plots were captured at distances of 50–100 m from LI plots under similar site conditions. These findings emphasize the critical need for long-term monitoring and effective management of *L. camara* to prevent its further spread and mitigate future ecological and biodiversity-related challenges.

5 Conclusion

In the present study, LI sites had lower diversity and biomass C stocks in tree juveniles and herbs but higher SOC and litter C compared to UI sites. The density of *L. camara* was negatively correlated with plant diversity, tree juvenile C, herb C, and total ecosystem C storage, while it was positively correlated with litter C and SOC. These findings reveal that plant species richness and C pools tend to be altered by invasion, which has important implications for C cycling. As *L. camara* reduces tree regeneration, it could gradually shift diversity patterns across the landscape. Furthermore, although shrub biomass may increase due to *L. camara* invasion, the reduction in tree regeneration is likely to disrupt the overall balance of ecosystem-level C pool partitioning in the long run. This study improves our understanding of how shrub invasion impacts diversity and ecosystem-level carbon storage, highlighting the need for long-term monitoring, conservation, and restoration efforts to mitigate these effects.

To effectively manage the spread of this invasive shrub, an integrated approach should be adopted, involving a thorough analysis of the cost–benefit dynamics and the ecological and socioeconomic consequences. Additionally, more research is needed to understand periodic changes in plant diversity and C pool partitioning following *L.* removal, which could inform more effective management and restoration strategies.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary materials](#), further inquiries can be directed to the corresponding author/s.

Author contributions

PL: Data curation, Formal analysis, Investigation, Project administration, Software, Writing – original draft, Writing – review & editing. SK: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. JD: Data curation, Formal analysis, Investigation, Project administration, Software, Writing – original draft, Writing – review &

editing, Conceptualization, Funding acquisition, Methodology, Resources, Supervision, Validation, Visualization. KH: Formal analysis, Writing – review & editing. MK: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2025.1412130/full#supplementary-material>

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