Invasive shrub *Lantana camara* L. alters the flora and soils in tropical dry deciduous forests of Central India

Parvaiz Ahmad Lone 1 | Javid Ahmad Dar 1,2 | Subashree Kothandaraman 1 | Mohammed Latif Khan 1

1Forest Ecology and Ecosystems Laboratory, Department of Botany, Dr. Harisingh Gour Vishwavidyalaya (A Central University), Sagar, India
2Department of Environmental Science, School of Engineering and Applied Sciences, SRM University-AP, Guntur, India

**Correspondence**
Mohammed Latif Khan, Forest Ecology and Ecosystems Laboratory, Department of Botany, Dr. Harisingh Gour Vishwavidyalaya (A Central University), Sagar, Madhya Pradesh 470003, India. Email: khanml61@gmail.com

**Funding information**
This study was supported by Science and Engineering Research Board (SERB), Department of Science and Technology, New Delhi, under National Post-Doctoral Fellowship Scheme (Ref. No.: PDF/2015/000447) to the second author. We would also like to thank the Department of Biotechnology, Government of India (No. BT/PR12899/NDB/39/506/2015 dt. 20/06/2017), for partial funding.

**Associate Editor:** Jennifer Powers

**Handling Editor:** Asmita Sengupta

**Abstract**

*Lantana camara* (hereafter *Lantana*) is a highly noxious invasive weed species of global concern. However, its impacts on floristic and soil properties in tropical dry deciduous forests are elusive and fragmented. We aimed to assess the changes in the flora and soil properties following the invasion by *Lantana* in Central Indian forest ecosystems. Three study sites were selected, and each site was further divided into two subsites: *Lantana*-invaded (LI) and uninvaded (UI). In total, 60 plots of 0.25 ha each (10 plots in each subsite) were laid randomly. Within each plot, floristic structure, composition, diversity, soil organic carbon (SOC), soil total nitrogen (STN), moisture (M%), pH, and bulk density (BD) were assessed. *Lantana*-invaded sites showed a significant decrease in density (D), basal area (BA), species richness (SR), and evenness (E) of saplings (<3 cm diameter at breast height [DBH]), juveniles (between 3 and 9.9 cm DBH), and herbs. In LI sites, a reduction of 57% and 25% was observed in lower DBH class of trees (saplings and juveniles). In all the LI sites, significant increase in SOC, STN, and M%, and a significant decrease in pH were recorded. *Lantana* may greatly impact the vegetation and soil properties, and successively, these strong changes may increase its invasive potential and ability to replace native species by averting their natural regeneration potential. Therefore, a proper management strategy of this noxious weed is imperative to prevent its further expansion and future problems.

**Keywords**
Central India, composition, diversity, *Lantana camara*, soils, stand structure, tropical forests

1 | INTRODUCTION

Biological invasions are a major threat to global biodiversity and have significant ecological impacts in a wide range of ecosystems (Seebens et al., 2017; Stinca et al., 2020). Invasive species are the second biggest threat to biodiversity loss after habitat fragmentation (Ahmad et al., 2019; Simberloff et al., 2013) as they pose detrimental impacts on the native local biodiversity, ecosystems, economy, and human health (Hejda et al., 2009; Ramírez-Albores et al., 2019). They are found in almost all terrestrial ecosystems and are important drivers of global change biology (Vitousek, 1994). Invasive species impact ecosystems by altering the fire regimes, geomorphology (Fei et al., 2014; Gaertner et al., 2014) and have substantial impacts on both ecosystem structure and functioning, such as reduction in native species diversity, changes in ecosystem productivity, and alteration of soil nutrient pools (Pysek et al., 2012).

Numerous mechanisms have been identified by which plants alter the physical, chemical, and biological properties of soils...
Many involve changes in the quantity, quality, and/or timing of inputs of plant-derived substrate; others may result from changes in microclimate associated with changes in density and height of the vegetation, or changes in water relations (Sharma & Raghubanshi, 2009). In addition to the potential underlying mechanisms of Lantana camara (hereafter Lantana) colonization, the contemporary reports on changes in density and Lantana proliferation (Prasad, 2010; Ramaswami & Sukumar, 2014) indicate the possible role of other mechanisms operating at a larger scale, for example, extended drought or stochastic rainfall. Furthermore, the effect of other local-scale factors, for example, biotic interactions, soil, and topography are also considered as possible mechanisms underlying invasion (Sharma & Raghubanshi, 2011). The success of invasive plants is due to its particular traits such as phenotypic plasticity, short-life spans, pollination by generalists, high fecundity, rapid growth rates, and allelopathy. (Rejmánek, 1995).

Tropical forests are known to have rich species diversity and tropical dry forests are the most endangered and degraded of all ecosystems in the world (Janzen, 1998). There is a growing consensus that invasive plants create "novel" tropical ecosystems with vegetation transitions (Seastedt et al., 2008). Furthermore, shifts in vegetation transitions are often accompanied by alterations in soil physico-chemical properties (Ehrenfeld, 2010) that lead to further degradation. The facilitation of invasion by forest degradation is often overlooked, particularly in the tropical forests of developing countries such as India (Mungi et al., 2020). Globally, Lantana removal experiments have been shown to promote native tree diversity and avian diversity (Lambert et al., 2016; Safari & Byarugaba, 2008). However, as Lantana is not the only factor shaping forest communities, successful restoration requires that Lantana removal should be accompanied with other suitable measures and long-term monitoring of interactions is necessary (Lambert et al., 2017; Yeates & Schooeler, 2011). Despite the numerous studies on the impacts of invasive species, only a few have studied the impacts on diversity, vegetation structure, and soil properties in forests (Dobhal et al., 2011; Kumar et al., 2020; Sharma & Raghubanshi, 2009, 2010; Sundaram & Hiremath, 2012).

Lantana is a vigorously growing shrub that is highly invasive with 650 varieties in over 60 countries (Global Invasive Species Database, 2020). It is widespread covering about 13 million hectares (Goyal et al., 2018; Sharma et al., 2005) and threatens 44% of the total Indian forests (Mungi et al., 2020). It has spread in almost all the dry deciduous forests of India (Sharma & Raghubanshi, 2006). Most of the past studies have centered on the effects of invasion on the herbaceous and seedling vegetation, and the research on the impacts of invasive species on vegetation composition, diversity, and soil properties in tropical dry deciduous forests of India, particularly in Central Indian forests is scarce and fragmented. We predict that Lantana invasion (1) affects diversity, composition, and vegetation structure of multiple life forms, viz. tree saplings, juveniles, adults, herbs, and shrubs and lianas, and (2) alters the soil physico-chemical properties in tropical dry deciduous forests of Central India.

2 | MATERIALS AND METHODS

2.1 | Study species

Lantana camara L. (Verbenaceae) is a woody shrub native to Central and South America and is regarded as one of the ten worst invasive species in the world (Richardson & Rejmanek, 2011). It was introduced as an ornamental hedge plant in East India Company Botanical Gardens in Calcutta in 1809, from where it escaped and became invasive (Kannan et al., 2013). The plant is profusely branched and grows up to 2–4 m high in open unshaded sunny environments (Day et al., 2003), and as a liana up to 15 m when light intensity is low (Lowe et al., 2000). It is shade-tolerant and produces 10,000–12,000 fruits (Kohli et al., 2006) and is very commonly distributed across fragmented dry forests in Central India (Mungi et al., 2020).

2.2 | Study area description

The present study was conducted in three forest study sites (Kesli, Deori and Shahgarh ranges) located between 21°17′–26°52′N and 78°08′–82°49′E in the district Sagar of Madhya Pradesh (M.P), Central India (Table 1, Figure 1). The area is covered by Vindhyachal mountain range at an average height of 420 m asl. The forest in the area belongs to group 4b of the Champion and Seth’s classification (Champion & Seth, 1968), and the climate is subtropical with hot dry summers (March to mid-June), monsoon season (mid-June to September) and, cool and dry winters (October–February). The area receives an annual average rainfall of 1197.6 mm of which approximately 90% takes place during the southwest monsoon. The mean annual minimum and maximum temperatures vary between 11.6 and 40.7°C in January and May, respectively. The major soil types of the area are clay loam, sandy clay loam, and sandy loam. The vegetation of the area is characterized by tropical dry deciduous forests, dominated by Tectona grandis, Diospyros melanoxylon, Butea monosperma, and Lagerstroemia parviflora. During the last few decades, these forests have been subjected to anthropogenic disturbances such as grazing, felling and lopping for timber, fodder, and fuelwood collection, which lowered the canopy density and increased the light availability. This led the forests to be severely infested by plant invasions, particularly Lantana (Dar et al., 2019) which impacted the physical, chemical, and biological aspects of ecosystems (Lone et al., 2019).

2.3 | Vegetation sampling design

A reconnaissance survey of the entire region was carried out, three study sites were selected, and each site was divided into two subsites (Lantana-invaded [LI] and uninvaded [UI]). The LI subsites were selected, having Lantana cover/density >50%, whereas UI subsites were selected with no or very less Lantana cover. The phytosociological attributes such as species richness,
diversity, density, frequency, basal area, and size class distribution were studied during the peak growing period (August–October) in 2017 and 2018. In each subsite, 10 square plots of 50 m x 50 m were laid randomly. The UI plots were chosen in neighboring localities at >50–100 m away from LI plots with similar site conditions. Each 50 m x 50 m plot was further sub-gridded into 25 (10 m x 10 m) quadrats to enumerate trees. In addition, 10 quadrats (5 m x 5 m) and 10 sub-quadrats (1 m x 1 m) were laid to enumerate the shrubs and herbs, respectively (Kershaw, 1964; Misra, 1968). The tree individuals were classified as follows: seedlings (<3 cm DBH, diameter at breast height), juveniles (between 3 and 9.9 cm DBH), and adults (>10 cm DBH). A total of 60 plots (50 m x 50 m) were laid in the three study sites. In each quadrat, all the tree individuals at 1.37 m above the ground were measured and shrub diameter was recorded at >10 cm above the ground level. Herbaceous individuals were counted and measured with digital Vernier caliper. Vegetation composition was evaluated by analyzing the density (D), basal area (BA), abundance, frequency, and Importance Value Index (IVI) following Curtis and McIntosh (1951) and Walkley and Black (1934). 

Another set of soil samples were collected from each study site to estimate bulk density (BD). Three sets of undisturbed soil cores were taken from each plot. The samples were oven-dried at 105 ± 5°C for 72 h and re-weighed. The coarse fragments were separated by sieving, and the samples were re-weighed. Soil BD was calculated following Pearson et al. (2005):

\[ \text{BD (g m}^{-3}) = \frac{\text{Oven dry mass (g m}^{-3})}{\text{Core volume (m}^3) - \text{Mass of coarse fragments (g)}}/2.65 \text{ (g cm}^{-3}) \]

where 2.65 was taken as a constant for the density of rock fragments (g cm\(^{-3}\)).

The total C content of 0–10 cm soil depth was estimated following Pearson et al. (2005):

\[ \text{SOC (Mg C ha}^{-1}) = [(\text{BD (g m}^{-3}) \times \text{soil depth (cm) \times C})] \times 100 \]

Soil moisture (M%) was measured by the gravimetric method. Soil pH (1:2.5 ratio of soil: water) was measured with digital pH meter. Three replicates were tested for each forest plot (30 per subsite).
2.5 | Statistical analysis

A t-test was performed to compare the differences in means of species richness, density, basal area, diversity indices, and soil properties, and Tukey's HSD test \(p < .05\) was performed using SPSS 20.0. Diversity indices and box plots were computed and drawn using PAST 3.1 (Hammer et al., 2001, Natural History Museum, University of Oslo). Linear correlations were done to assess the relationships of Lantana densities with soil properties and vegetation attributes (species richness, density, and basal area). Bonferroni corrections were done to reduce multiple comparisons.

3 | RESULTS

3.1 | Impact on species richness and diversity

A decline in species richness (SR) and diversity was observed with increase in Lantana density. The LI sites had a significantly lower \(p < .05\) SR with 98 species when compared with UI sites (132). In LI sites, the SR of sapling, juvenile, and adult trees ranged from 1–5, 3–15 and 3–14, whereas in UI sites, it ranged from 1–9, 2–14 and 4–16, respectively. The mean SR of saplings (13), juveniles (30), and adult trees (29) were significantly \(p < .05\) lower in LI sites than the saplings (21), juveniles (33) and adult trees (40) in UI sites. The herbaceous SR ranged from 16–36 and 12–26 in UI and LI sites, respectively, and the mean SR was significantly \(p < .001\) lower in LI (53) than UI (72) sites, whereas the SR of shrubs and lianas were also significantly \(p < .05\) lower in LI sites (7) than UI sites (13). The total SR was 55, 72, and 54 in LI sites and 71, 98, and 76 in UI sites for saplings, juveniles, and adults, respectively (Figures 2–5, Figure S1). In total, 141 plant species (49 trees, 78 herbs, 14 shrubs, and lianas) from 122 genera and 44 families were documented in all the three study sites (Table S1). Eighty-nine species (63.1%) were found common to both UI and LI sites, while 43 species (30.5%) occur only in UI sites and nine species (6.4%) occur only in LI sites (Table 2).

The values of Shannon’s \(H'\) and Simpson’s dominance indices \(Cd\) of trees were significantly \(p < .05\) lower in LI than UI sites (Figures 2–5). The \(H'\) ranged from 0.35–1.81, 0.41–2.00, 0.46–2.12,
and 1.77–3.03 in UI sites, and from 0.51–1.61, 0.66–2.08, 0.50–1.91, and 1.80–2.60 in LI sites for saplings, juveniles, adults, and herbs, respectively. The Cd of saplings, juveniles, adult tree species, and herbs ranged from 0.19–0.80, 0.18–0.76, 0.14–0.83, and 0.06–0.25 in UI sites and 0.20–0.65, 0.16–0.64, 0.21–0.76, and 0.09–0.30 in LI sites, respectively. The evenness index (E) was higher in LI sites than in UI sites. The E of saplings, juveniles, and adult tree species ranged from 0.45–0.89, 0.28–0.75 and 0.18–0.69 in UI sites and 0.60–0.95, 0.29–0.77 and 0.31–0.79 in LI sites, respectively. The herb E was significantly ($p < .05$) higher in LI sites than in UI sites, and it ranged 0.33–0.71 in UI and 0.33–0.76 in LI sites. The Margalef’s index (R) of tree saplings, herbs, and total plants was significantly ($p < .001$) reduced in LI than in UI sites (Figures 2–5, Figure S1).

### 3.2 Impact on density and basal area

A significant impact of *Lantana* density (No. ha$^{-1}$) was observed on the density (No. ha$^{-1}$) and basal area (m$^2$ ha$^{-1}$) of tree and herbaceous vegetation (Table S1). The density of tree saplings and juveniles decreased significantly ($p < .001$) with increase in *Lantana* density, whereas the adult tree density did not show any significant trend (Figures 2–5, Figure S1). The tree density of saplings and juveniles ranged from 4–308 and 4–100 individuals ha$^{-1}$ in UI and 104–1336 and 132–732 individuals ha$^{-1}$ in LI sites, respectively. The mean densities of saplings and juveniles were also reduced significantly ($p < .001$) with *Lantana* density and were higher in UI sites (109 & 623) than in LI (29 & 373) sites. The adult tree density ranged from 312–664 and 248–424 individuals ha$^{-1}$ in UI and LI sites, with the mean of 456 and 331 individuals ha$^{-1}$, respectively. The total tree density (saplings + juveniles + adults) also showed a significant ($p < .001$) declining trend in LI than in UI sites. The total tree density in LI sites reduced significantly ($p < .05$) and ranged from 452–1116 individuals ha$^{-1}$ (mean 734 individuals ha$^{-1}$) and in UI sites from 528–1960 individuals ha$^{-1}$ (mean 1118 individuals ha$^{-1}$). The mean herb density declined significantly ($p < .001$) in LI sites than in UI sites. The herb density ranged from 289,000–640,000 individuals ha$^{-1}$ (mean of 451,866 individuals ha$^{-1}$) in UI and 188,000–373,000 individuals ha$^{-1}$ (mean 284,466 individuals ha$^{-1}$) in LI sites.

The basal area of saplings and juveniles decreased significantly ($p < .001$) with increase in Lantana density, whereas the adult basal area did not show any significant trend. The basal area of saplings and juveniles declined significantly ($p < .001$) in LI sites and ranged from 0.00–0.02 and 0.34–2.09 m$^2$ ha$^{-1}$ (mean 0.05 and 1.89 m$^2$ ha$^{-1}$) in UI sites, and 0.01–0.15 and 0.43–4.29 m$^2$ ha$^{-1}$ (mean 0.01 and 1.21 m$^2$ ha$^{-1}$) in LI sites. The adult tree basal area ranged from 14.5–30.3 and 11.5–23.4 m$^2$ ha$^{-1}$ in UI and LI sites with the mean of 19.7 and 14.7 m$^2$ ha$^{-1}$, respectively (Figures 2–5, Figure S1). The total tree basal area was reduced significantly ($p < .01$) in LI sites and ranged from 13.5–24.1 m$^2$ ha$^{-1}$ and in UI sites from 15.2–33.1 m$^2$ ha$^{-1}$, with the mean of 15.9 and 21.6 m$^2$ ha$^{-1}$, respectively. The mean herb basal area declined significantly ($p < .001$) in LI sites when compared with UI sites. The herb basal area ranged from 4.3–9.2 and 2.6–7.1 m$^2$ ha$^{-1}$ in UI and LI sites, with the mean of 6.7 and 4.8 m$^2$ ha$^{-1}$, respectively.
3.3 | Impact on family composition

The number of species in a family and the number of families were observed to decline in relation to *Lantana* density. The number of species in a family varied from 1–17 and 1–13 in UI and LI sites, respectively. Forty-three species from 7 families and 9 species from 2 families were found only in UI and LI sites, respectively. Out of 141 species, 89 species (35 families) were common to both UI and LI.
sites. Fabaceae (17 (UI) and 13 (LI) species), Poaceae (12 (UI) and 9 (LI) species), Asteraceae (8 (UI) and 6 (LI) species), Malvaceae (7 (UI) and 6 (LI) species), and Acanthaceae (6 (UI) and 4 (LI) species) were the most speciose families (Table 2).

### 3.4 Impact on diameter class distribution

*Lantana* density was associated with changes in diameter class distribution of trees. Tree density of lower diameter class (<3 DBH) was reduced by 57% in LI sites followed by 25% and 23%, of 3.1–10 and 30.1–40 DBH classes, respectively (Figure 6). Tree density decreased significantly (*p* < .001) with increase in diameter class in both UI and LI sites. The highest density of 51.8% was contributed by 3.1–10 cm diameter class, and lowest of 0.7% density was contributed by >50 cm diameter class.

### 3.5 Impacts on the soil properties

*Lantana* density was related to changes in soil properties. The values of BD (g cm⁻³) and pH were significantly (*F* = 12.96, *p* < .05) lower in LI than in UI sites, whereas M% was significantly (*F* = 68.55, *p* < .001) higher in LI than in UI sites (Figure 7). The SOC and STN stocks were significantly (*F* = 48.3, *p* < .001; *F* = 51.7, *p* < .001) higher in LI than in UI sites (Figure 7).

### 3.6 Correlations of *Lantana* density with other variables

*Lantana* density was significantly negatively correlated with SR, density, and basal area of tree saplings and herb density (*p* < .001, Table 3). Non-significant negative correlations were observed with SR of juveniles, adults, total trees, and herbs; densities of tree juveniles and total trees; and basal area of tree juveniles, adults, and total trees. The SOC, STN, and M% showed significant positive correlations, whereas soil pH showed a significant negative correlation with *Lantana* density. Soil BD had a non-significant negative relationship with *Lantana* density (Table 3).

## 4 DISCUSSION

Comparing invaded and uninvaded sites helps us to measure the impact of invasive species on the native resident communities (Levine et al., 2003). In the present study, a significant (*p* < .05) decrease in SR and diversity was observed with increase in *Lantana* density. Localities with *Lantana* invasion are known to have lower SR than uninvaded localities (Dobhal et al., 2011; Sharma & Raghubanshi, 2010). It is therefore evident that *Lantana* successfully establishes itself and competitively excludes the resident plant communities in the studied sites. The variation in SR among the sites could be because native species differ in their resistance to invasion.
TABLE 2  Family-wise contribution of genera (G), species (S), and density (D; stems ha⁻¹) in uninvaded (UI) and *Lantana*-invaded (LI) sites in tropical dry deciduous forests of Sagar, Madhya Pradesh, India

| Families        | Uninvaded (UI) |            |            | Lantana-invaded (LI) |            |            |
|-----------------|----------------|------------|------------|----------------------|------------|------------|
|                 | Site-1         | Site-2     | Site-3     | Site-1              | Site-2     | Site-3     |
|                 | G | S | D | G | S | D | G | S | D | G | S | D | G | S | D | G | S | D |
| Acanthaceae     | 3 | 3 | 35,400 | 6 | 6 | 70,432 | 2 | 2 | 31,400 | 2 | 2 | 14,400 | 4 | 4 | 50,400 | 2 | 2 | 21,600 |
| Amarantaceae    | 2 | 2 | 2800 | 2 | 2 | 13,400 | 1 | 1 | 2800 | 1 | 1 | 1600 | 2 | 2 | 12,000 | 1 | 1 | 2400 |
| Anacardiaceae   | 3 | 3 | 39 | 4 | 4 | 72 | 2 | 2 | 44 | 2 | 2 | 21 | 3 | 3 | 53 | 2 | 2 | 12 |
| Annonaceae      | 1 | 1 | 67 | 2 | 2 | 236 | 1 | 1 | 20 | 1 | 1 | 70 | 1 | 1 | 10 |
| Apiceae         | 1 | 1 | 600 | 1 | 1 | 2480 | 3 | 3 | 1405 | 1 | 1 | 496 | 3 | 3 | 1048 | 3 | 3 | 1213 |
| Apocynaceae     | 1 | 1 | 576 | 1 | 1 | 2480 | 3 | 3 | 1405 | 1 | 1 | 496 | 3 | 3 | 1048 | 3 | 3 | 1213 |
| Aristolochiaceae| 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 |
| Asteraceae      | 6 | 6 | 53,648 | 5 | 5 | 30,200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 |
| Boraginaceae    | 1 | 1 | 400 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 |
| Burseraceae     | 1 | 1 | 33 | 1 | 1 | 20 | 1 | 1 | 10 | 1 | 1 | 5 | 1 | 1 | 5 | 1 | 1 | 5 |
| Celastraceae    | 2 | 2 | 33 | 2 | 2 | 401 | 1 | 1 | 32 | 1 | 1 | 224 | 1 | 1 | 224 | 1 | 1 | 224 |
| Cochlospermaceae| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Combretaceae    | 2 | 2 | 70 | 2 | 2 | 40 | 2 | 2 | 45 | 2 | 2 | 53 | 2 | 2 | 22 | 2 | 2 | 8 |
| Commelinaceae   | 1 | 1 | 200 | 1 | 1 | 600 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 | 1 | 1 | 200 |
| Convolvulaceae  | 1 | 1 | 400 | 1 | 2 | 71,600 | 2 | 2 | 2200 | 2 | 2 | 35,800 | 1 | 1 | 200 |
| Cucurbitaceae   | 1 | 1 | 400 | 1 | 1 | 1800 | 1 | 1 | 1200 | 1 | 1 | 2000 | 1 | 1 | 200 |
| Cyperaceae      | 1 | 1 | 2000 | 1 | 1 | 1200 | 1 | 1 | 2000 | 1 | 1 | 2000 | 1 | 1 | 200 |
| Ebenaceae       | 1 | 1 | 111 | 1 | 1 | 606 | 1 | 1 | 606 | 1 | 1 | 44 | 1 | 1 | 310 | 1 | 1 | 40 |
| Euphorbiaceae   | 1 | 1 | 10,800 | 1 | 1 | 3600 | 1 | 2 | 400 | 1 | 1 | 900 | 1 | 1 | 1000 | 1 | 1 | 1200 |
| Fabaceae        | 9 | 13 | 134,142 | 12 | 17 | 133,200 | 9 | 13 | 53,340 | 6 | 10 | 59,468 | 10 | 13 | 43,075 | 6 | 8 | 39,301 |
| Hypoxidaceae    | 1 | 1 | 6200 | 1 | 1 | 1200 | 1 | 1 | 1200 | 1 | 1 | 1200 | 1 | 1 | 1200 |
| Lamiaceae       | 2 | 2 | 1542 | 2 | 2 | 953 | 3 | 3 | 2198 | 2 | 2 | 6403 | 1 | 1 | 362 | 1 | 1 | 248 |
| Loganiaceae     | 1 | 1 | 1400 | 1 | 1 | 1400 | 1 | 1 | 1400 | 1 | 1 | 1400 | 1 | 1 | 1400 |
| Lythraceae      | 1 | 1 | 51 | 1 | 1 | 54 | 1 | 1 | 67 | 1 | 1 | 85 | 1 | 1 | 5 | 1 | 1 | 59 |
| Malvaceae       | 4 | 4 | 59,200 | 7 | 7 | 37,436 | 4 | 4 | 31,600 | 3 | 4 | 46,800 | 5 | 6 | 29,402 | 4 | 6 | 45,200 |
| Meliaceae       | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Menispermaceae  | 1 | 1 | 1000 | 2 | 2 | 6400 | 1 | 1 | 400 | 1 | 1 | 2000 | 1 | 1 | 1200 |
| Molluginaceae   | 1 | 1 | 400 | 1 | 1 | 400 | 1 | 1 | 400 | 1 | 1 | 400 | 1 | 1 | 400 |
| Moraceae        | 1 | 1 | 1 | 1 | 1 | 8 | 1 | 2 | 3 | 1 | 1 | 7 | 1 | 1 | 7 | 1 | 1 | 7 |

(Continues)
TABLE 2 (Continued)

| Families           | Uninvaded (UI) | Lantana-invaded (LI) |
|--------------------|----------------|----------------------|
|                    | Site-1 G S D   | Site-2 G S D |
|                    | Site-1 G S D   | Site-2 G S D |
|                    | Site-3 G S D   | Site-3 G S D |
|                    | Site-3 G S D   | Site-3 G S D |
| Myrtaceae          | 1 1 136        | 1 1 1600 |
| Oxalidaceae        | 1 1 5600       | 1 1 10,000 |
| Phyllanthaceae     | 2 4 2004       | 1 5 10,804 |
| Poaceae            | 9 9 146,400    | 9 9 97,000 |
| Polygalaceae       | 1 1 1000       | 1 1 18 |
| Rhamnaceae         | 1 1 16         | 1 1 1 |
| Rubiaceae          | 5 5 1403       | 1 1 2 |
| Rutaceae           | 1 1 2          | 1 1 2 |
| Salicaceae         | 1 1 39         | 1 1 2 |
| Sapindaceae        | 1 1 1          | 1 1 3 |
| Sapotaceae         | 1 1 1          | 1 1 1 |
| Scrophulariaceae   |                | 1 1 10,800 |
| Solanaceae         | 1 1 400        | 1 1 2 |
| Ulmaceae           | 1 1 1          | 1 1 1 |
| Verbenaceae        | 1 1 96         | 1 1 128 |
| Violaceae          | 1 1 12         | 1 1 18 |
| Vitaceae           | 1 1 48         | 1 1 1 |

Note: The table continues with data for other families and sites.
where some species are more easily excluded than others in invaded sites (Stinson et al., 2007). About 33%, 8%, 26%, 25%, 43%, and 24% decline in SR were observed in saplings, juveniles, adults, herbs, shrubs and lianas, and total species, respectively in LI sites. Increase in Lantana density causes pervasive losses in SR across multiple life forms (Sharma & Raghubanshi, 2010). The highest decline in SR was observed in the case of tree saplings, juveniles, and herbs. This could be because Lantana produces copious light-weight seeds with high adaptability that enables them to grow vigorously and suppress the growth of native plant species. Furthermore, the release of allelochemicals from its roots also hampers the growth of native plants (Kumar et al., 2020).

The values of Shannon index were lower in LI sites than UI sites for all the life forms and significantly in case of saplings, juveniles, and herbs. Lantana invasion is often associated with significant decreases in plant species richness, diversity, and evenness in deciduous forest types (Badalamenti et al., 2016). The evenness index increased in LI sites for tree saplings, but decreased for shrub and lianas. Changes in evenness of an ecosystem may impact the productivity, resistance to invasion, and local plant extinction rates (Wilsey & Potvin, 2000). The impact of invasion largely depends on the degree of dominance (Pyšek & Pyšek, 1995). Overall, the values of dominance index were lower in LI sites than UI sites.

The species compositional changes induced by Lantana invasion are primarily driven by gradual changes in vegetation structure (Gooden et al., 2009). In this study, Lantana density was associated with changes in vegetation attributes. The density of tree saplings, juveniles, and herbaceous vegetation was reduced significantly ($p < .001$) with increase in Lantana density. The frequency of occurrence of some tree species decreased in LI sites compared with UI sites. However, the density of shrub and lianas was greater in LI sites than in UI sites due to higher Lantana density. Overall, Lantana invasion suppresses the growth of trees by impacting the younger stages of development, viz. sapling and juvenile stages, whereas the adult trees remained largely unaffected. Lantana is unlikely to displace tree individuals that have attained adult stage and the stage of development determines the resistance/susceptibility of a particular species to invasion (Gentle & Duggin, 1997). For example, if a species is mainly represented by saplings in a particular location, it is easily susceptible and might eventually be displaced, but if it contains several adult individuals, it would resist invasion and is unlikely to get displaced (Gooden et al., 2009). Such variations in species density due to invasion by Lantana gradually alter landscape-level heterogeneity (Vitousek et al., 1996).

Invasion by Lantana has significantly ($p < .001$) lowered the basal area of tree saplings, juveniles, and herbs in LI sites compared with UI sites. This might be due to the formation of thick Lantana thickets that alter the microenvironment (light and temperature) inhibiting germination or growth (Sharma & Raghubanshi, 2007). Furthermore, at the ground level, there occurs accumulation of Lantana litter which also cause allelopathic suppression of growth and recruitment of saplings, juveniles, and herbs (Gentle & Duggin, 1997). The changes in quantitative ecological parameters such as density, basal area, and IVI by invasion of Lantana lead to alteration in plant assemblage patterns and forest structure, which may eventually create demographic instability (Sharma & Raghubanshi, 2010).

Lantana density was associated with decline in the number of families. The number of families was slightly lower in LI sites (39) when compared with UI sites (44). With unabated invasion of Lantana in the studied sites, the number of families would continue to decrease with decrease in SR and local extinctions. Fabaceae, Poaceae, and Asteraceae were the most speciose families. Large families such as these are often the most well-represented and widely distributed in nature (Panda et al., 2013; Subashree et al., 2020).

Analysis of tree size class distribution reveals the population structure of a forest (Newbery & Gartlan, 1996). The composition and density distribution of saplings and juveniles indicate the future structure of the forest (Myo et al., 2016). A population structure comprising of an ample number of saplings and juveniles indicates...
good regeneration behavior, while their insufficient numbers denote poor regeneration (Saxena & Singh, 1985). In this study, tree density declined significantly \((p < .001)\) with increase in diameter class in LI sites than in UI sites (Figure 6). This trend indicates that the tree species in the studied sites possess a good regenerative capacity. Even so, tree saplings and tree juveniles were the most impacted life forms by *Lantana* invasion and further expansion of this species could affect their regenerative potential. *Lantana* is known to displace natural scrub communities and prevent natural regeneration of some tree species (Ambika et al., 2003; Sharma & Raghubanshi, 2006). The recruitment of small-sized tree individuals into larger diameter classes is also impeded by *Lantana* invasion (Alemu & Terefe, 2015; Murali & Setty, 2001). Although both UI and LI sites showed the same trend, UI sites had a higher number of small-sized tree individuals than the corresponding LI sites. This indicates that regenerative potential decreased post *Lantana* invasion.

The impacts of *Lantana* invasion were also reflected in the soil physico-chemical properties of the studied sites. While BD and pH were significantly \((p < .001)\) lower in LI sites than in UI sites, M%, SOC, and STN showed significant \((p < .001)\) opposite trends. The observed pattern is consistent with the findings of Niu et al. (2007), Dogra et al. (2009) and Kumar et al. (2020). Invaded habitats experience changes in plant species composition and community structure, and this alteration leads to changes in soil properties and nutrient dynamics (Rusterholz et al., 2018). *Lantana* density increases litter

**FIGURE 7** (a) Soil organic carbon (SOC; mg C ha\(^{-1}\)), (b) soil total nitrogen (STN; mg C ha\(^{-1}\)), (c) moisture (M; %), (d) pH, and (e) bulk density (BD; g cm\(^{-3}\)) in uninvaded (UI) and *Lantana*-invaded (LI) sites. Different letters show significantly \((p < .05)\) different means between them by Tukey’s HSD post hoc test.
inputs, and its chemical composition is also different from the native forest litter. The high SOC, STN, and M% of the Lantana litter and favorable microclimate beneath Lantana canopy support faster decomposition and release of N. These alterations in litter inputs and chemistry significantly alter SOC, STN, and M% in soils (Sharma & Raghubanshi, 2009). The significantly higher M% in the soil of LI sites could be due to the presence of more debris and organic matter from dead Lantana leaves, which decompose slowly (Fan et al., 2010; Singh et al., 2014). Lantana produces a substantial quantity of litter rich in allelochemicals which might react with organic matter and affect soil property (Ruwanza et al., 2013). Allelochemicals are usually released from roots, shoots, leaves, or flowers, which negatively affect the neighboring native species (Rice, 1974). The effects of allelochemicals are usually greater in the introduced range than in the native range (Inderjit et al., 2011). Soil BD and pH were lower in LI sites than in UI sites which could be due to higher litter content and its decomposition by micro-organisms. Similar results have been observed in tropical dry deciduous forests by Sharma and Raghubanshi (2009). The altered soil properties provide favorable conditions for further invasion by Lantana and other invasive species (Niu et al., 2007). Lantana invasion not only affects the native resident plant community structure and composition, but also changes the soil physico-chemical properties that may not be suitable for their growth.

The SR, density, and basal area of tree saplings and herb density showed significant negative relationships with Lantana density, whereas negative non-significant correlations were observed with SR of juveniles, adults, total trees, and herbs; densities of tree juveniles and total trees; and basal area of tree juveniles, adults, and total trees (Table 3). The SOC, STN and M% showed significant positive correlations with Lantana density, whereas pH showed a significant negative relationship (Table 3). Similar findings were recorded by Badalamenti et al. (2016) in Mediterranean ecosystems. Lantana density was significantly positively correlated with shrub and liana density (p ≤ .01), which is due to its dominance in the shrub and liana category. Invasive plants are known to alter soil pools and ecosystem processes by changing the organic matter inputs, decomposition, and mineralization (Ashton et al., 2005; Ruwanza & Shackleton, 2016). Changes in soil nutrients following Lantana invasion could be a contributor to its successful proliferation. Levine et al. (2006) also opined that such increase in nutrients positively affect the growth and spread of the invader in the form of the "push and pull" theory of invasion.

The studied sites are open forests and are exposed to frequent grazing, illegal felling of trees for timber, fuel, and fodder, have canopy openings, variability in light, drought, and fires (Kumar et al., 2020; Sharma & Raghubanshi, 2006). Thus, these disturbances trigger changes in community structure, composition, and microclimate conditions, which could help in the successful proliferation of Lantana. The pervasive threat posed by Lantana to native vegetation at the scale of individual forest types, as well as at a larger landscape-level has long-term consequences for forest structure and composition (Sundaram & Hiremath, 2012). Some forest types may be more vulnerable to invasion than others, while communities vary in their responses to invasion (Hejda et al., 2009). Therefore, in heterogeneous landscapes, it is necessary to examine the response of community variables to invasive species at both at the scales of landscape-level as well as that of individual forest types (Sundaram & Hiremath, 2012). Based on these findings as well as other studies (Prasad, 2010; Ramaswami & Sukumar, 2011, 2013; Sharma & Raghubanshi, 2007), it is expected that after accounting for the influence of rainfall, terrain, slope, altitude, fire frequency, and tree density, the SR of tree species would decrease as Lantana cover increased.

The disturbance factors such as fires, livestock grazing, illegal felling of trees, canopy openness, and drought in the low diversity/density study sites will lead to lower diversity/density values and facilitate invasion, which would further lead to decline in diversity/density. Increased species richness might confer resistance to Lantana invasion through greater community stability, resilience to disturbance, and a more complete utilization of light, space, and nutrient resources through niche partitioning (Tilman et al., 2006). This is confirmed by empirical and correlative
evidence that Lantana invasion is inhibited by intact undisturbed vegetation (Prasad, 2012). Native species richness remains stable at lower density levels, but declines rapidly above the threshold level, which leads to compositional change. Thus, sparse Lantana cover has little effect on the resident community, with impacts elicited at an advanced stage of invasion. Potentially, broad-scale conservation of species diversity could be achieved by maintaining Lantana infestations below the threshold cover at sites containing regionally common species that are also widely represented in non-invaded vegetation. Furthermore, Lantana removal programs that also consider the local site conditions (Lambert et al., 2016; Yeates & Schooller, 2011) are essential for effective restoration of these forests.

5 | CONCLUSION

The present study revealed a significant negative impact of L. camara on diversity and vegetation attributes of native plant communities in the tropical dry deciduous forests of Central India. It is clear that Lantana-invaded sites comprise significantly lower richness, density, and basal area than uninvaded sites. Lantana invasion not only affects the vegetation, but also alters the soil properties favoring its own growth. Furthermore, the alterations in vegetation structure, composition, and soil properties could lead to changes in ecosystem functioning. Appropriate methods and long-term monitoring studies in permanent plots are needed for better understanding, management, and restoration of the invaded landscapes in tropical forests.

AUTHORS’ CONTRIBUTION

The study was conceptualized and designed by PAL, JAD, SK, and MLK. Material preparation, field work, data collection, and analysis were performed by PAL, JAD, and SK. The first draft of the manuscript was written by PAL, JAD, and SK. MLK provided review and comments. All the authors have read and approved the submitted version of the manuscript.

ACKNOWLEDGMENTS

We are thankful to the Madhya Pradesh State Forest Department and Forest Department of Sagar district for permission and for providing the necessary facilities and staff support during the field work. We also thank Prof. Pramod Kumar Khare, Department of Botany, for the identification of plant specimens.

CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.sj3tx966t (Lone et al., 2022).

ORCID

Parvaiz Ahmad Lone https://orcid.org/0000-0002-8642-0609
Javid Ahmad Dar https://orcid.org/0000-0002-2018-8376
Subashree Kothandaraman https://orcid.org/0000-0002-7940-7705
Mohammed Latif Khan https://orcid.org/0000-0001-6849-0307

REFERENCES

Ahmad, R., Khuroo, A. A., Hamid, M., & Rashid, I. (2019). Plant invasion alters the physico-chemical dynamics of soil system: Insights from invasive Leucanthemum vulgare in the Indian Himalaya. Environmental Monitoring Assessment, 191, 792. https://doi.org/10.1007/s10661-019-7683-x
Alemu, S. C., & Terefe, A. A. (2015). Impact of invasion: A case study on the ecological and socioeconomic impact of Lantana camara (L.) in Abay Millennium Park (AMP), Bahir Dar, Ethiopia. Journal of Ecology and the Natural Environment, 7, 132–145. https://doi.org/10.5897/JENE2015.0514
Ambika, S. R., Poornima, S., Palaniraj, R., Sati, S. C., & Narwal, S. S. (2003). Allelopathic plants. 10. Lantana camara L. Allelopathy Journal, 12(2), 147–162.
Angiosperm Phylogeny Group IV (APG IV) (2019). http://www.mobot.org/MOBOT/research/APweb/
Ashton, I. W., Hyatt, L. A., Howe, K. M., Gurevitch, J., & Lerdau, M. T. (2005). Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecological Applications, 15(4), 1263–1272. https://doi.org/10.1890/04-0741
Badalamenti, E., Gristina, L., Laudicina, V. A., Novara, A., Pasta, S., & Mantia, T. L. (2016). The impact of Carpobrotus cf. Acinaciformis (L.) L. bolus on soil nutrients, microbial communities structure and native plant communities in Mediterranean ecosystems. Plant and Soil, 409, 19–34. https://doi.org/10.1007/s11104-016-2924-z
Binkley, D., & Sollins, P. (1990). Factors determining differences in soil pH in adjacent conifer and alder-conifer stands. Soil Science Society of America Journal, 54, 1427–1433. https://doi.org/10.2136/sssaj1990.03615995005400050036x
Champion, H. G., & Seth, S. K. (1968). A revised survey of the forest types of India (p. 404). Govt. of India Press.
Curtis, J. T., & McIntosh, R. P. (1951). An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology, 32(3), 476–496. https://doi.org/10.2307/1931725
Dar, J. A., Subashree, K., Sundarapandian, S., Saikia, P., Kumar, A., Khare, P. K., Dayanandan, S., & Khan, M. L. (2019). Invasive species and their impact on tropical forests of Central India: A review. In S. Garkoti, S. Van Bloem, P. Fulé, & R. Semwal (Eds), Tropical ecosystems: Structure, functions and challenges in the face of global change (pp. 69–109). Springer. https://doi.org/10.1007/978-81-930-8249-9_5
Day, M. D., Wiley, C. J., Playford, J., & Zalucki, M. P. (2003). Lantana: Current management status and future prospects. ACIAR. https://aciar.gov.au/publication/books-and-manuals/lantana-current-management-status-and-future-prospects
Dobhal, P. K., Kohli, R. K., & Batish, D. R. (2011). Impact of Lantana camara L. invasion on riparian vegetation of Nayar region in Garhwal Himalayas. Journal Ecology Natural Environment, 3, 11–22.
Dogra, K. S., Kohli, R. K., & Sood, S. K. (2009). An assessment and impacts of three invasive species in the Shivalik hills of Himachal Pradesh, India. International Journal Biodiversity Conservation, 1(1), 004–010.
Ehrenfeld, J. G. (2010). Ecosystem consequences of biological invasions. Annual Review of Ecology, Evolution, and Systematics, 41, 59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650
Fan, L., Chen, Y., Yuan, J., & Yang, Z. (2010). The effect of Lantana camara Linn. Invasion on soil chemical and microbiological properties
Ruwanza, S., Gaertner, M., Richardson, D. M., & Esler, K. J. (2013). Soil
Sharma, G. P., & Raghubanshi, A. S. (2010). How lantana invades dry
Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E.,
Seastedt, T. R., Hobbs, R. J., & Suding, K. N. (2008). Management of novel
Saxena, A. K., & Singh, J. S. (1985). Tree population structure of certain
Ruwanza, S., & Shackleton, C. M. (2016). Effects of the invasive shrub,
Lantana camara, on soil properties in the eastern cape, South Africa.
https://doi.org/10.1016/j.actao.2018.08.004
Rustinholz, H. P., Schneuwly, J., & Baur, B. (2018). Invasion of the alien
Lantana camara L. invasion in the Vindhyan tropical dry deciduous forest of India. Lyonia, 11(1), 27–39.
Sharma, G. P., & Raghubanshi, A. S. (2007). Effect of Lantana camara L.
cover on local depletion of tree population in the Vindhyan tropical
dry deciduous forest of India. Applied Ecology Environmental Research, 5(1), 109–121.
Sharma, G. P., & Raghubanshi, A. S. (2009). Lantana invasion alters
soil nitrogen pools and processes in the tropical dry deciduous
forest of India. Applied Soil Ecology, 42(2), 134–140. https://doi.
org/10.1016/j.apsis.2009.03.002
Sharma, G. P., & Raghubanshi, A. S. (2011). Lantana camara L. invasion
and impact on herb layer diversity and soil properties in a dry
deciduous forest of India. Applied Ecology and Environmental Research, 9(3), 253–264.
Sharma, G. P., Raghubanshi, A. S., & Singh, J. S. (2005). Lantana invasion:
An overview. Weed Biology Management, 5(4), 157–165. https://doi.
org/1111/j.1445-6664.2005.00178.x
Simberloff, D., Louis Martin, J., Genovese, P., Maris, V., Wardle, D. A.,
Aronson, J., Courchamp, F., Galli, B., García-Berthou, E., Pascal,
M., Pyšek, P., Sousa, R., Tabacchi, E., & Vilà, M. (2013). Impacts
of biological invasions: what’s what and the way forward. Trends
in Ecology & Evolution, 28(1), 58–66. https://doi.org/10.1016/j.
tree.2012.07.013
Singh, H. P., Batish, D. R., Dogra, K. S., Kaur, S., Kohli, R. K., & Negi, A.
(2014). Negative effect of litter of invasive weed Lantana camara on
structure and composition of vegetation in the lower Siwalik Hills,
northern India. Environmental Monitoring Assessment, 186, 3379–
3389. https://doi.org/10.1007/s10661-014-3624-x
Stevens PF (2017) Angiosperm phylogeny website. Version 14. http://www.
mobot.org/MOBOT/research/APweb/
Stinca, A., Acosta, A. T. R., Adorni, M., Alleffi, M., Allegrezza, M.,
Angiolini, C., Assini, S., Bagella, S., Bonari, G., Bovio, M., Bracco, F.,
Brundu, G., Caccianiga, M., Carnevali, L., Di Cecco, V., Ceschin, S.,
Ciasmetti, G., Cogoni, A., Foggi, B., ... Lastrucci, L. (2020). Impact
of invasive alien plants on native plant communities and Natura
2000 habitats: State of the art, gap analysis and perspectives in
Italy. Journal of Environmental Management, 274, 111140. https:
doi.org/10.1016/j.jenvman.2020.111140
Stinson, K., Kaufman, S., Durbin, L., & Lowenstein, F. (2007). Impacts
of garlic mustard invasion on a forest understory community. Northeastern Naturalist, 14(1), 73–88. https://doi.
org/10.1656/1092-6194(2007)14[73:OGMII]2.0.CO;2
Subashree, K., Dar, J. A., Karuppusamy, S., & Sundarapandian, S. M.
(2020). Plant diversity, structure and regeneration potential in tropical
forests of Western Ghats, India. Acta Ecologica Sinica, 41, 259–
284. https://doi.org/10.1656/1092-6194(2007)00000001.001
Sundaram, B., & Hiremath, A. J. (2012). Lantana camara invasion in a
heterogeneous landscape: Patterns of spread and correlation with changes in native vegetation. Biological Invasions, 14, 1127–1141.
https://doi.org/10.1007/s10530-011-0144-2
Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem
stability in a decade-long grassland experiment. Nature, 441, 629–632.
https://doi.org/10.1038/nature04742
Vitousek, P. M. (1994). Beyond global warming: Ecology and global change.
Ecology, 75(7), 1861–1876. https://doi.org/10.2307/1941591
Vitousek, P. M., D’Antonio, C. M., Loope, L. L., & Westbrooks, R. (1996).
Biological invasions as global environmental change. American Scientist, 84, 468–478. https://www.jstor.org/stabl
e/29775751
Walkey, A., & Black, I. A. (1934). An examination of the Degtjareff
method for determining soil organic matter, and a proposed modification
of the chromic acid titration method. Soil Science, 37, 29–38.
https://doi.org/10.1007/00010694-193401000-00003
Wiersema, J. H. (2019). GRIN taxonomy. US National Plant Germplasm
System. Checklist Dataset. https://doi.org/10.15468/a014pp
Wilsey, B. J., & Potvin, C. (2000). Biodiversity and ecosystem functioning: Importance of species evenness in an old field. Ecology, 81, 887–892. https://doi.org/10.1890/0012-9658(2000)081[0887:BAEFIO]2.0.CO;2

Yeates, A. G., & Schooler, S. S. (2011). Influence of Lantana camara and its removal on tree dynamics in a recently burnt wet sclerophyll forest in northern NSW. Ecological Management & Restoration, 12(3), 236–241. https://doi.org/10.1111/j.1442-8903.2011.00600.x

SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.