

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

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Abstract

Background and Aims

Lantana camara 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 camara* in Central Indian forest ecosystems.

Methods

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 and soil SOC, STN, M%, pH and bulk density were assessed.

Results

Lantana-invaded sites showed a significant decrease in density (D), basal area (BA), species richness (SR) and evenness (E) of seedlings (< 3cm diameter at breast height (DBH)), juveniles (> 3-9.9cm DBH), and herbs. In LI sites, a reduction of 57 and 25% has been observed in lower DBH class of trees (< 3cm and > 3-9.9cm). In all LI sites, a significant increase of soil organic carbon (SOC), soil total nitrogen (STN) and soil moisture (M%) and a significant decrease of pH and bulk density (BD) were recorded.

Conclusions

Lantana may greatly impact the vegetation and soil properties and, successively, these strong changes 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.

Introduction

Biological invasions are a major threat to global biodiversity and have greater ecological impacts in a wide range of ecosystems worldwide (Seebens et al. 2017; Lazzaro et al. 2020). Invasive species are the second biggest threat to biodiversity loss after habitat fragmentation (Simberloff et al. 2013; Ahmad et al. 2019) as they pose detrimental impacts on the native local biodiversity, ecosystems, economy and human health (D'Antonio and Vitousek 1992; Levine et al., 2003; Hejda and Pysek 2006; 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 (Liao et al. 2008; Pysek et al. 2012; Barney et al. 2015).

Invasive species are often perceived as those species that were introduced in a particular location intentionally or unintentionally that penetrates and replaces the prevailing indigenous vegetation of a location (Rejmanek 1995) and are known to have a wide range of ecological impacts on introduced ecosystems such as competitive exclusion of native species, increased water loss, alterations in nutrient dynamics, fire regimes, etc. (Truscott et al 2008). Invasion by alien plant species alters the native community structure and composition, cause local extinctions of resident species, alter several ecological processes, successional rates and trajectories (Vila et al. 2011; Potgieter et al. 2014; Bellard et al. 2016). Invasive plants not only alter the structural and functional diversity of ecosystems, but also change the properties of soils, such as pH, moisture, bulk density, soil organic carbon, total nitrogen, phosphorus and other soil micro-biota (Ehrenfeld, 2003; Dassonville et al., 2008; Sharma and Raghubanshi 2009; Timsina et al. 2011;). The success of invasive plants is often due to its particular traits such as phenotypic plasticity, short-life spans, pollination by generalists, high fecundity, rapid growth rates, allelopathy, etc. (Rejmanek 1995). Invasive plants can trigger new complex interactions with the existing native species and also with other co-invading species (Hartman and McCarthy 2008). As invasive species drastically alter the structure and functioning of ecosystems, in the changing global climatic warming, the rising rate of plant invasions are regarded as a major threat to the global biodiversity (Hellmann et al. 2008; Catford et al. 2012; Taylor et al. 2012).

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 1988; Cabin et al. 2002). Several invasive species are able to establish viable populations in mature tropical forests and are a cause of concern (Brown et al. 2006). The tropical dry forests have canopy openings, grazing, fires etc., that act as windows for invasive species proliferation (Johnstone 1986; Raghubanshi and Tripathi 2009). There is a growing consensus that invasive plants create 'novel' tropical ecosystems with vegetation transitions (Veldman and Putz 2010). Furthermore, shifts in vegetation transitions are often accompanied by alterations in soil physico-chemical properties due to changes in the timing, duration, quality and quantity of plant-derived organic substrates (Ehrenfeld et al. 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).

Despite the numerous studies on the impacts of invasive species, only few have studied their impacts on the vegetation structure, composition, diversity, and soil properties in tropical and temperate forest ecosystems (Sharma and Raghubanshi 2009; Sundaram and Hiremath 2012; Sharma and Raghubanshi 2010; Dobhal et al. 2011; Kumar et al. 2020). Assessing the impacts on the structural and functional diversity is important, because they are influenced by each other, and the changes in vegetation structure, composition and diversity due to invasions would eventually result in alterations in soil properties and vice-versa (Vitousek, 1990)

Alike to many invasive plants, *Lantana camara* is a vigorously growing shrub that is highly invasive in over 60 countries with about 650 varieties (Global Invasive Species Database 2020). It is widespread throughout the tropical, subtropical and warm temperate regions covering about 13 million hectares (Sharma et al. 2005; Goyal et al. 2018) and a major threat to 44% of the total Indian forests (Mungi et al. 2020). It has almost spread in all the dry deciduous forests of India (Sharma and Raghubanshi 2006). Most of the past studies have centered on the effects of invasion on the herbaceous and seeding 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. To bridge this gap, the present study has been aimed: 1) to examine the impact of *L. camara* on the vegetation structure, composition and diversity of tree saplings, juveniles, adults, herbs and shrubs & lianas, and 2) the impact of *L. camara* on soil properties in tropical dry deciduous forests of Central India.

Materials And Methods

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 and 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 (Kohli et al. 2006; Kannan et al. 2013). The plant is profusely branched and grows up to 2–4 meters (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 landscapes in fragmented dry deciduous forests of Central India (Mungi et al. 2020).

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 district Sagar of Madhya Pradesh (M.P), Central India (Table 1, Fig. 1). The area is situated in the north central region of M.P. and is covered by Vindhyanal 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 and 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 to 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 11.6–40.7°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, predominated by species of *Tectona grandis*, *Diospyros melanoxylon*, *Butea monosperma* and *Lagerstroemia parviflora*. During the last few decades, these forests have been severely infested by plant invasions, particularly *Lantana* (Dar et al. 2019) and impacted the physical, chemical and biological aspects of ecosystems (Lone et al. 2019).

Table 1
Study site characteristics of uninvaded (UI) and *Lantana*-invaded (LI) sites of tropical dry deciduous forest of Sagar, Madhya Pradesh

Parameter	Uninvaded (UI)			<i>Lantana</i> -invaded (LI)		
	Site-1	Site-2	Site-3	Site-1	Site-2	Site-3
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
No. of plots	10	10	10	10	10	10
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
Mean tree DBH	20.96	19.8	22.2	21.4	19.3	23.3
Max. tree DBH	128.2	113.5	75.1	71.8	57.5	124.8
Tree species richness	21	30	17	13	24	17
Genera	20	29	16	12	22	17
Families	13	17	11	8	13	12
Soil pH (0–10 cm)	6.22	6.4	6.2	5.82	6.14	6.05
Soil moisture % (0–10 cm)	20.3	19.6	15.8	22.6	22.2	17.9
Bulk density g cm ⁻³ (0–10 cm)	1.06	1.12	1.17	0.89	0.98	1.1

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%. The phytosociological analysis was done in peak growing period during August to October in 2017 and 2018. In each subsite, 10 square plots of 50 m × 50 m were laid randomly in LI and UI localities. The UI plots were chosen in neighbouring localities at > 50–100 m away from LI plots with similar site conditions. Each 50 m × 50 m plot was further sub-gridded into 25 (10 m × 10 m), 10 (5 m × 5 m) and 10 (1 m × 1 m) quadrats for trees, shrubs and herbs, respectively (Kershaw 1964; Misra 1968). The enumerated individuals of trees were classified into three categories: saplings (< 3 cm DBH, diameter at breast height), juveniles (> 3–9.9 cm DBH), and adults (≥ 10 cm DBH). A total of 60 plots (50 m × 50 m) were laid for trees, 60 (5 m × 5 m) for shrubs and herbs respectively (10 in each subsite). In each quadrat, all the tree individuals > 3 cm DBH at 1.37 m above the ground were measured, shrub diameter was recorded at > 10 cm above the ground level and individuals were counted. Herbaceous species individuals were counted and measured with digital Vernier caliper. Vegetation composition was evaluated by analysing the density (D), basal area (BA), abundance, frequency, and Importance Value Index (IVI) following Misra (1968) and Curtis and McIntosh (1951). Diameter class-wise distributions were calculated for each subsite. The plant specimens were prepared and identified at Department of Botany, Dr. Harisingh Gour Vishwavidyalaya (A Central University), Sagar, with the help of Flora of Bhopal (Oommachan, 1977) and other standard floras. The assignment of a species to the family was done as per Angiosperm Phylogeny Group IV (APG IV) system of classification (Stevens, 2017). The plant names and the corresponding author citations were given following GRIN (Germplasm Resources Information Network) Taxonomy and Global Biodiversity Information Facility (Wiersema, 2019).

Study sites and soil sampling

From each plot, soil samples were collected at five random points to a depth of 10 cm using a soil core sampler of 5 cm internal diameter. These samples were mixed thoroughly, and 250 g were collected, air dried, and stored in airtight polyethylene bags and sent to the laboratory for further analysis. The composite soil samples were sieved through a 2 mm stainless steel sieve using a mortar and pestle. Soil organic carbon (SOC) was estimated following Walkley and Black's method (Walkley 1934), which is a widely used procedure (Pearson et al. 2005). The total soil nitrogen (STN) was calculated using semi-micro Kjeldahl method (Kirk 1950).

Soil bulk density was calculated by following Pearson et al. (2005).

$$\text{Bulkdensity}(\text{g}/\text{m}^3) = \frac{\text{Ovendrymass}(\text{g}/\text{m}^3)}{\text{Corevolume}(\text{m}^3) - (\text{Massofcoarsefragments}(\text{g})/2.65(\text{g}/\text{cm}^3))}$$

where 2.65 was taken as a constant for the density of rock fragments (g/cm³)

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

$$\text{SOC}(\text{Mg C}/\text{ha}) = [(\text{soil bulk density}(\text{g}/\text{m}^3) \times \text{soil depth}(\text{cm}) \times \text{C})] \times 100$$

Soil moisture (%) 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 each subsite).

Statistical analysis

Statistical analysis was done by analysis of variance (one-way ANOVA). Differences in means of species richness, density, basal area, diversity indices and soil properties were tested by Tukey's HSD test (at $p < 0.05$) using SPSS version 20.0. Diversity indices and box plots were computed and drawn using the Past 3.1 program (version 3.1; Øyvind Hammer, Natural History Museum, University of Oslo). The linear correlation regression was done for assessing the relationship between *Lantana* densities with soil parameters and other predictor variables.

Results

Impact on species richness and diversity

In total, 141 plant species (49 trees, 78 herbs, 14 shrubs and lianas) from 122 genera and 44 families including *L. camara* were documented in all the three study sites (Table 2). The total species richness (SR) was significantly ($p < 0.05$) lower in LI sites (98) than in UI sites (132). In LI sites (Kesli, Deori and Shahgarh), 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 sapling (13), juvenile (30) and adult trees (29) were significantly ($p < 0.05$) lower in LI sites than the sapling (21), juvenile (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 ($p < 0.001$) lower in LI (53) than UI (72) sites, whereas, the SR of shrubs and lianas were also significantly ($p < 0.05$) lower in LI sites (7) than UI sites (13). The total SR in LI sites were 55, 72 and 54, and in UI sites were 71, 98 and 76 for saplings, juveniles and adults respectively (Figs. 3–7). A reduction of -33, -8, -26, -25, -43 and -24% in SR of saplings, juveniles, adults, herbs, shrubs & lianas and total SR respectively, has been observed in LI sites compared to UI sites (Fig. 2). 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 9 species (6.4%) only in LI sites (Table 3).

Table 2

Density (No. ha⁻¹), basal area (m² ha⁻¹) and Importance Value Index (IVI) of different life forms in uninvaded (UI) and *Lantana*-invaded (LI) sites of tr

Life form	Density						Basal area						
	Uninvaded (UI)			Lantana-invaded (LI)			Uninvaded (UI)			Lantana-invaded (LI)			
Saplings	Site-1	Site-2	Site-3	Site-1	Site-2	Site-3	Site-1	Site-2	Site-3	Site-1	Site-2	Site-3	
<i>Acacia catechu</i> (L.f.) Willd.					1							0.0004	
<i>Acacia leucophloea</i> (Roxb.) Willd.		1			1			0.0004				0.0003	
<i>Aegle marmelos</i> (L.) Correa		2	1					0.0010	0.0003				
<i>Anogeissus latifolia</i> (DC.) Wallich ex Guill. & Perr.	6		1				0.0034		0.0003				
<i>Bauhinia racemosa</i> Lam.					1							0.0005	
<i>Bridelia retusa</i> (L.) A.Juss.		1						0.0004					
<i>Buchanania lanzan</i> Spreng		3						0.0014					
<i>Butea monosperma</i> (Lam.) Taub.	3	1			2		0.0019	0.0003				0.0006	
<i>Cassia fistula</i> L.		5	4		6	6		0.0022	0.0014			0.0026	0.003
<i>Dalbergia paniculata</i> (Roxb)		6						0.0022					
<i>Diospyros melanoxylon</i> Roxb	10	75	2	2	24	1	0.0058	0.0358	0.0010	0.0017	0.0116	0.000	
<i>Flacourtia indica</i> (Burm. f.) Merr.			2						0.0010				
<i>Garuga pinnata</i> Roxb.	9			2			0.0043			0.0010			
<i>Grewia tiliifolia</i> Vahl. var. tiliifolia		2						0.0007					
<i>Kydia calycina</i> Roxb.		1						0.0005					
<i>Lagerstroemia parviflora</i> Roxb	6	6	2	2		1	0.0031	0.0030	0.0015	0.0010		0.000	
<i>Miliusa tomentosa</i> (Roxb.) J. Sinclair	12	45			3	2	0.0069	0.0222			0.0018	0.001	
<i>Ougeinia oojeinensis</i> (Roxb.) Hochr.		2						0.0011					
<i>Schleichera oleosa</i> (Lour.) Oken.		4			1			0.0018				0.0004	
<i>Semecarpus anacardium</i> L.f.	1							0.0004					
<i>Syzygium cumini</i> (L.) Skeel		42						0.0206					
<i>Tectona grandis</i> L.f.	26	26	21	1	8	17	0.0131	0.0117	0.0115	0.0006	0.0040	0.007	
<i>Terminalia tomentosa</i> Wight & Arn.						2						0.000	
<i>Wrightia tinctora</i> (Roxb)			1		4	3			0.0005		0.0022	0.001	
Juveniles													
<i>Acacia catechu</i> (L.f.) Willd.			2	2	3				0.0082	0.0102	0.0034		
<i>Acacia leucophloea</i> (Roxb.) Willd.	7	3	1	13	3		0.0249	0.0079	0.0043	0.0446	0.0110		
<i>Aegle marmelos</i> (L.) Correa		1	9	2	4	3		0.0017	0.0302	0.0071	0.0081	0.020	
<i>Annona squamosa</i> L.		9						0.0195					
<i>Anogeissus latifolia</i> (DC.) Wallich ex Guill. & Perr.	24	0	3	23	1		0.0716		0.0101	0.0890	0.0006		
<i>Azadirachta indica</i> A.Juss.				1						0.0015			
<i>Bauhinia racemosa</i> Lam.	1	8	1	2	3		0.0024	0.0370	0.0031	0.0060	0.0112		
<i>Bridelia retusa</i> (L.) A.Juss.	2	2		2			0.0024	0.0122		0.0118			
<i>Buchanania lanzan</i> Spreng	4	17	7	0	7	1	0.0213	0.0665	0.0236		0.0361	0.004	

Life form	Density						Basal area					
	Uninvaded (UI)		Lantana-invaded (LI)				Uninvaded (UI)		Lantana-invaded (LI)			
<i>Butea monosperma</i> (Lam.) Taub.	94	11	28	9	10	0.2992	0.0366	0.0968	0.0316	0.040		
<i>Casearia tomentosa</i> Roxb.				1						0.0010		
<i>Cassia fistula</i> L.	5	19	6	2	7	24	0.0078	0.0658	0.0233	0.0055	0.0248	0.058
<i>Chloroxylon swietenia</i> (Roxb.) DC.				2							0.0073	
<i>Cochlospermum religiosum</i> (L.) Alston		1		1			0.0048				0.0041	
<i>Cordia myxa</i> L.		2					0.0046					
<i>Dalbergia paniculata</i> (Roxb)		2					0.0061					
<i>Diospyros melanoxylon</i> Roxb	98	453	60	40	233	22	0.2103	1.3520	0.2482	0.1034	0.7482	0.091
<i>Elaeodendron Glaucum</i> (Rottb.) Pers.		1					0.0052					
<i>Ficus glomerata</i> Roxb.		3		2			0.0139				0.0022	
<i>Flacourtia indica</i> (Burm. f.) Merr.			18			5		0.0681				0.019
<i>Garuga pinnata</i> Roxb.	22			19	3		0.0284		0.0453	0.0097		
<i>Grewia tiliifolia</i> Vahl. var. tilifolia				2							0.0014	
<i>Holoptelea integrifolia</i> Planch.	1			1	1		0.0006		0.0016	0.0006		
<i>Kydia calycina</i> Roxb.		1					0.0013					
<i>Lagerstroemia parviflora</i> Roxb.	42	32	19	74	4	17	0.1055	0.0884	0.0706	0.2519	0.0140	0.048
<i>Lannea coromandelica</i> (Houtt.) Merr.	1			1			0.0031				0.0059	
<i>Madhuca indica</i> J.F.Gmel.	1			1			0.0024				0.0031	
<i>Miliusa tomentosa</i> (Roxb.) J. Sinclair	53	144		20	52	6	0.0916	0.4086		0.0548	0.1520	0.011
<i>Ougeinia oojeinensis</i> (Roxb.) Hochr.						2						0.007
<i>Schleichera oleosa</i> (Lour.) Oken.	2	18		1	2		0.0046	0.0531		0.0043	0.0055	
<i>Semecarpus anacardium</i> L.f.	14	1		7			0.0413	0.0020		0.0219		
<i>Syzygium cumini</i> (L.) Skeel		84					0.1953					
<i>Tectona grandis</i> L.f.	278	171	75	134	197	102	1.0394	0.5264	0.2020	0.5010	0.6474	0.275
<i>Terminalia arjuna</i> (Roxb.) Wight & Arn.		2					0.0074					
<i>Terminalia tomentosa</i> Wight & Arn.	18	5	2	3	1	2	0.0555	0.0204	0.0056	0.0134	0.0023	0.005
<i>Wrightia tinctora</i> (Roxb.)			10		4	6		0.0267			0.0053	0.018
<i>Ziziphus jujuba</i> Mill.			1					0.0035				
<i>Ziziphus xylopyrus</i> (Retz.) Willd.		1		2	2	1	0.0050		0.0058	0.0069	0.000	
Adults												
<i>Acacia catechu</i> (L.f.) Willd.	2		1	2	2		0.0406		0.0198	0.0131	0.1006	
<i>Acacia leucophloea</i> (Roxb.) Willd.	1	6	2	2	10	2	0.0333	0.2878	0.2420	0.0435	0.5120	0.098
<i>Adina cordifolia</i> (Roxb.) Brandis		1					0.0360					
<i>Aegle marmelos</i> (L.) Correa	2	1	11			18	0.0404	0.0746	0.4550			0.839

Life form	Density						Basal area					
	Uninvaded (UI)			Lantana-invaded (LI)			Uninvaded (UI)			Lantana-invaded (LI)		
<i>Albizia procera</i> (Roxb.) Benth	1			1			0.0343			0.1178		
<i>Anogeissus latifolia</i> (DC.) Wallich ex Guill. & Perr.	17	1	20	26	3	2	0.3968	0.1213	0.9170	1.0131	0.2772	0.048
<i>Bauhinia racemosa</i> Lam.	1	13		1	6		0.0156	0.2771		0.0141	0.1747	
<i>Bridelia retusa</i> (L.) A.Juss.		2						0.1049				
<i>Buchanania lanzan</i> Spreng	8	44	35		34	5	0.2773	1.1584	1.3821		1.1994	0.221
<i>Butea monosperma</i> (Lam.) Taub.	26	10	74	16	15	50	0.7311	0.3445	4.3461	0.2450	0.6686	3.910
<i>Cassia fistula</i> L.		2			1	4			0.0381		0.0087	0.071
<i>Chloroxylon swietenia</i> (Roxb.) DC.		1						0.0149				
<i>Cordia myxa</i> L.					2						0.1154	
<i>Dalbergia paniculata</i> (Roxb)	1		4		2		0.2454		0.4004		0.1186	
<i>Diospyros melanoxylon</i> Roxb.	3	78	56	2	53	17	0.0850	1.7044	1.7453	0.0161	1.0829	0.433
<i>Elaeodendron Glaucum</i> (Rottb.) Pers.	1							0.0097				
<i>Feronia elephantum</i> Corrêa		1							0.0390			
<i>Ficus glomerata</i> Roxb.		5							0.2366			
<i>Ficus religiosa</i> L.	1				1	7	1.0329				0.0513	2.386
<i>Flacourtia indica</i> (Burm. f.) Merr.		1	19			7		0.0336	0.3883			0.228
<i>Gardenia latifolia</i> Aiton		1			5			0.0602			0.3101	
<i>Garuga pinnata</i> Roxb.	2			1	2		0.1690			0.0103	0.0244	
<i>Holoptelea integrifolia</i> Planch.		1						0.0136				
<i>Lagerstroemia parviflora</i> Roxb.	3	16	46	9	1	41	0.0975	0.3672	1.8021	0.1225	0.0454	2.032
<i>Lanea coromandelica</i> (Houtt.)Merr.	6	2	2	10	10	6	0.4475	0.1658	0.1873	0.6837	0.3668	0.442
<i>Madhuca indica</i> J.F.Gmel.		2			8			0.2371			0.7151	
<i>Mangifera indica</i> L.		1						0.0302				
<i>Miliusa tomentosa</i> (Roxb.) J. Sinclair	2	38			15	2	0.0790	0.9851			0.1783	0.033
<i>Mitragyna parvifolia</i> (Roxb.) Korth.		1						0.0450				
<i>Ougeinia oojeinensis</i> (Roxb.) Hochr.						3						0.207
<i>Phyllanthus emblica</i> L.	2		4			1	0.0166		0.3062			0.058
<i>Pterocarpus marsupium</i> Roxb.			2		2				0.0889		0.1142	
<i>Schleichera oleosa</i> (Lour.) Oken.	1	11		1	6		0.0094	0.3928		0.0066	0.3262	
<i>Semecarpus anacardium</i> L.f.	5	4		4	1		0.1417	0.1278		0.1772	0.0902	
<i>Syzygium cumini</i> (L.) Skeel		10						0.0137				
<i>Sterculia urens</i> Roxb.		1						0.3702				
<i>Tamarandus indicus</i> L.		1						0.0067				
<i>Tectona grandis</i> L.f.	438	156	102	268	157	129	18.3109	5.3130	4.3480	12.8335	4.6086	5.073
<i>Terminalia arjuna</i> (Roxb.) Wight & Am.		22			1			4.8882			0.1011	
<i>Terminalia tomentosa</i> Wight & Am.	5	10	19	1	16	2	0.3219	0.7619	1.5898	0.0078	1.0419	0.382

Life form	Density						Basal area						
	Uninvaded (UI)			Lantana-invaded (LI)			Uninvaded (UI)			Lantana-invaded (LI)			
<i>Wrightia tinctora</i> (Roxb)	2			4			0.0383			0.059			
<i>Ziziphus xylopyrus</i> (Retz.) Wild.	1						0.0076						
Shrubs and Lianas													
<i>Adhatoda vasica</i> Nees	32						0.0015						
<i>Carissa spinarum</i> var. <i>spinarum</i>	64						0.0048						
<i>Cayratia triflora</i> (L.) Domin	48			256			0.0004			0.001			
<i>Desmodium gangeticum</i> (L.) DC.	576			32			0.0027			0.0002			
<i>Helicteres isora</i> L.	32						0.0064						
<i>Hemidesmus indicus</i> (L.) R. Br.	576	2480	1328	496	624	704	0.0146	0.0556	0.0362	0.0075	0.0138	0.018	
<i>Ichnocarpus frutescens</i> (L.) W. T. Aiton (C)				416			496			0.0101			0.016
<i>Lantana camara</i> L.	96	112	128	16176	17440	14512	0.0090	0.0138	0.0437	2.6001	2.5138	1.622	
<i>Maytenus emarginata</i> (Willd.)	32	400		32	224	32	0.0068	0.5265		0.0033	0.2272	0.010	
<i>Phyllodium pulchellum</i> (L.)	144						0.0077						
<i>Solanum anguivi</i> Lam.	864						0.0772						
<i>Ventilago calyculata</i> Tul.	16	16	32	16			0.0771	0.0974	0.0033		0.0125		
<i>Xanthium strumarium</i> L.	48	48		176			0.0086		0.0081	0.0340			
<i>Ziziphus oenoplia</i> (L.) Miller	16						0.0199						
Herbs													
<i>Acanthospermum hispidum</i> DC.				400						0.0040			
<i>Achyranthes aspera</i> L.	200	1000	2800	200			2400	0.0088	0.0728	0.1944	0.0160	0.146	
<i>Ageratum conyzoides</i> L.	30800	10800	19600	7800	10000	4600	0.3592	0.2480	0.3440	0.1296	0.2432	0.084	
<i>Alternanthera sessilis</i> (L.) R. Br. ex DC.	2600	12400		1600	11800		0.0960	0.3280		0.0176	0.3376		
<i>Alysicarpus longifolius</i> Sensu Span., non Wight & Arn.	4800	18400		400	3800		0.0360	0.1664		0.0024	0.0416		
<i>Alysicarpus monilifer</i> (L.) DC.	5800	4200	2400			1200	1000	0.0464	0.0360	0.0360	0.0112	0.007	
<i>Andrographis echinoides</i> (L.) Nees	3800			200			0.0216			0.0016			
<i>Anisochilus camosus</i> (L.f.) Wall.	800	400					0.0160	0.0024					
<i>Apluda mutica</i> L.	11400			14600	1000		0.0424			0.0488	0.0056		
<i>Aristida depressa</i> Retz.	11600						0.0256						
<i>Aristolochia indica</i> L.	200						0.0104						
<i>Axonopus compressus</i> (Sw.) P.Beauv.	1000						0.0088						
<i>Bidens biternata</i> (Lour.) Merr. & Sherff	6200	800	7800			0.3448			0.0432	0.4984			
<i>Biophytum sensitivum</i> (L.) DC. var. <i>sesbanioides</i>	5600	10000		1600			0.1576	0.3712		0.0728			
<i>Blumea lacera</i> (Burm.f.) DC.	10200			400			0.3320			0.0160			
<i>Cajanus scarabaeoides</i> (L.) Thouars	3400						0.0360						
<i>Cassia pumila</i> Lam.	18000	8800	600	3200	600	1200	0.4592	0.1008	0.0112	0.0336	0.0128	0.010	
<i>Cassia tora</i> L.	30000	4000	36800	18800		32800	1.6424	0.1752	2.2440	1.0200	1.531		

Life form	Density					Basal area						
	Uninvaded (UI)			Lantana-invaded (LI)		Uninvaded (UI)			Lantana-invaded (LI)			
<i>Centella asiatica</i> (L.) Urb.	600					0.0008						
<i>Cissampelos pareira</i> L.	1000	5200	400	2000	1200	0.0056	0.0472	0.0048	0.0272	0.011		
<i>Cocculus hirsutus</i> (L.) Diels	1200					0.0112						
<i>Commelina benghalensis</i> L.	200	1200	600	200		0.0008	0.0104	0.0064	0.0024			
<i>Conyza canadensis</i> (L.) Cronquist	200					0.0000 0.0008						
<i>Corchorus trilocularis</i> L.	5000	4800	1200	1000	1000	0.1616	0.1384	0.0416	0.0328	0.022		
<i>Crotolaria juncea</i> L.	200					0.0128						
<i>Curculigo orchioides</i> Gaertn.	6200 1200				1000	0.1760 0.0344			0.028			
<i>Cynodon dactylon</i> (L.) Pers.	32200	20600		5000	8000	0.1296	0.0936	0.0320	0.0432			
<i>Cynoglossum furcatum</i> Wall.	400					0.0096						
<i>Cyperus rotundus</i> L.	2000	1800	1200	2000	200	0.0168	0.0136	0.0096	0.0168	0.003		
<i>Dactyloctenium aegyptium</i> (L.) Willd.	2200					600			0.0152 0.003			
<i>Desmodium triflorum</i> (L.) DC.	72000	93000	15200	34600	37000	4200	0.2912	0.4056	0.0664	0.1384	0.1624	0.022
<i>Dichanthium annulatum</i> (Forssk.) Stapf.	1400	1000	800	2400		600	0.0048	0.0072	0.0040	0.0136	0.003	
<i>Digitaria sanguinalis</i> (L.) Scop.	600 2000			0.0024 0.0248								
<i>Elephantopus scaber</i> Auct. non L.	400	3200	5800	4600	4400	0.0152	0.1400	0.2816	0.2000	0.194		
<i>Eleusine indica</i> (L.) Gaertn.	5600	1000	1400	1600		0.0216	0.0048	0.0112	0.0072			
<i>Emilia sonchifolia</i> (L.) DC. ex Wight	2200					200			0.0080 0.0008			
<i>Eragrostis unioides</i> (Retz.) Nees ex Steud	2000 2200			1000			0.0064 0.0040			0.001		
<i>Euphorbia hirta</i> L.	10800	3600	2800	9000	1000	1200	0.2208	0.0768	0.0552	0.1656	0.0168	0.009
<i>Euphorbia hypericifolia</i> L.	1400					0.0160						
<i>Evolvulus alsinoides</i> (L.)	400					0.0024						
<i>Evolvulus nummularius</i> (L.)	71200			1600	35200	0.1712			0.0088	0.092		
<i>Heteropogon contortus</i> (L.) P.Beauv. ex Roem. & Schult.	12000	19200		7400	15800		0.1112	0.1480	0.0448	0.1208		
<i>Hibiscus lobatus</i> (Murray) Kuntze	1800		400	200	200	0.0456			0.0160	0.0016	0.002	
<i>Hyptis suaveolens</i> (L.) Poit.	600		1600	6000	0.0288			0.0776	0.2680			
<i>Indigofera cordifolia</i> Roth	600					0.0088						
<i>Ionidium suffruticosum</i> (L.) Ging. in DC.	400					0.0048						
<i>Ipomoea cairica</i> (L.) Sweet	600			600	0.0040 0.005							
<i>Justicia quinqueangularis</i> Koen. ex Roxb.	16000	7400		4800	1000	0.1368 0.0624			0.0480	0.0096		
<i>Lindernia ciliata</i> (Colsm.) Pennell	2200					0.1152						
<i>Lindernia crustacea</i> (L.) F. Muell.	8600					0.0568						
<i>Melothria heterophylla</i> (Lour.) Cogn.	400					0.0024						
<i>Merremia emarginata</i> (Burm. fil.) Hall. fil.	400					0.0008						
<i>Mollugo oppositifolia</i> L.	400			200	0.0056			0.0024				

Life form	Density						Basal area					
	Uninvaded (UI)		Lantana-invaded (LI)				Uninvaded (UI)		Lantana-invaded (LI)			
<i>Oldenlandia herbacea</i> (L.)	1200						0.0024					
<i>Oplismenus burmannii</i> (Retz.) P.Beauv.	79600	85400	120400	58800	129600	95400	0.2152	0.2048	0.3048	0.1296	0.3296	0.220
<i>Parthenium hysterophorus</i> L.			10200		5000				0.6856		0.512	
<i>Peristrophe paniculata</i> (Forssk.) R.K. Brummitt	1000						0.0088					
<i>Phyllanthus fraternus</i> G.L.Webster	800	200					0.0136	0.0040				
<i>Phyllanthus niruri</i> L.	200	1600					0.0160	0.0808				
<i>Phyllanthus urinaria</i> L.	800	1200	3000			1000	0.0088	0.0216	0.0192			0.005
<i>Phyllanthus simplex</i> Retz.	1200	1200	6000	200	1200		0.0144	0.0152	0.0824		0.0024	0.016
<i>Physalis minima</i> L.	400	400					0.0256	0.0104				
<i>Polygala chinensis</i> L.	1000						0.0048					
<i>Ruellia tuberosa</i> L.	1600	11400	8400	19000	6000		0.0360	0.2032	0.1960	0.3408	0.160	
<i>Rungia pectinata</i> (L.)	17800	46800	23000	9600	30200	15600	0.1432	0.4624	0.2536	0.1008	0.3240	0.157
<i>Setaria viridis</i> (L.) P.Beauv.	400	2000	1200	1200			0.0024	0.0112	0.0088	0.0048		
<i>Sida acuta</i> Burm. f.			7800	6400	8600					0.4400	0.3152	0.446
<i>Sida cordifolia</i> L.	26400	23600	29600	20200	21000	31400	1.0152	0.5696	1.1200	0.8640	0.5576	1.154
<i>Sida rhombifolia</i> L.					2600							0.119
<i>Spermacoce hispida</i> Linn	200	2400					0.0024	0.0152				
<i>Spigelia anthelmia</i> L.			1400			200			0.0112			0.001
<i>Sporobolus diander</i> (Retz.) Beauv.	1600	3200	13000	2600	3400	2000	0.0024	0.0056	0.0184	0.0040	0.0064	0.003
<i>Themeda triandra</i> Forssk.	12600	11200	3400	3200			0.0640	0.0504	0.0208	0.0112		
<i>Tridax procumbens</i> L.	15000	5200	800	13400	3800	800	0.4792	0.2000	0.0184	0.3712	0.0952	0.028
<i>Triumfetta rhomboidea</i> Jacq.	26000	9000	400	17000	800	1400	1.3856	0.4912	0.0160	0.8824	0.0288	0.048
<i>Urena lobata</i> L.			1800							0.4576		
<i>Vernonia cinera</i> (L.)	1200	2400	600			0.0304			0.0472			0.0104
<i>Zornia diphylla</i> (L.)Pers.	3400	400	400			0.0160	0.0016					0.0032

Table 3

Family-wise contribution of genera (G), species (S) and density (D; No ha⁻¹) in uninvaded (UI) and *Lantana*-invaded (LI) sites in tropical dry deciduous forests of Sagar, Madhya Pradesh, India

Families	Uninvaded (UI)						Lantan-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	35400	6	6	70432	2	2	31400	2	2	14400	4	4	50400	2	2	21600
Amaranthaceae	2	2	2800	2	2	13400	1	1	2800	1	1	1600	2	2	12000	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
Apiaceae	1	1	600															
Apocynaceae	1	1	576	1	1	2480	3	3	1405	1	1	496	3	3	1048	3	3	1213
Aristolochiaceae							1	1	200									
Asteraceae	6	6	53648	5	5	30200	8	8	41248	6	6	29976	5	5	19200	4	4	14800
Boraginaceae	1	1	400	1	1	2							1	1	2			
Burseraceae	1	1	33							1	1	22	1	1	5			
Celastraceae	2	2	33	2	2	401				1	1	32	1	1	224	1	1	
Cochlospermaceae				1	1	1							1	1	1			
Combretaceae	2	2	70	2	3	40	2	2	45	2	2	53	2	3	22	2	2	8
Commalinaceae	1	1	200	1	1	1200	1	1	600	1	1	200						
Convolvulaceae	1	1	400				1	2	71600				2	2	2200	2	2	35800
Cucurbitaceae	1	1	400															
Cyperaceae	1	1	2000	1	1	1800	1	1	1200	1	1	2000				1	1	200
Ebenaceae	1	1	111	1	1	606	1	1	118	1	1	44	1	1	310	1	1	40
Euphorbiaceae	1	1	10800	1	1	3600	1	2	4200	1	1	9000	1	1	1000	1	1	1200
Fabaceae	9	13	134142	12	17	133200	9	13	53340	6	10	59468	10	13	43075	6	8	39301
Hypoxidaceae				1	1	6200	1	1	1200							1	1	1000
Lamiaceae	2	2	1542	2	2	953	3	3	2198	2	2	6403	1	1	362	1	1	248
Lythraceae	1	1	51	1	1	54	1	1	67	1	1	85	1	1	5	1	1	59
Malvaceae	4	4	59200	7	7	37436	4	4	31600	3	4	46800	5	6	29402	4	6	45200
Meliaceae										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	200			
Moraceae	1	1	1	1	1	8							1	2	3	1	1	7
Myrtaceae				1	1	136												
Oxalidaceae	1	1	5600	1	1	10000				1	1	1600						
Phyllanthaceae	2	4	2004	2	5	3405	1	5	10804	1	1	2	1	1	200	1	3	2201
Poaceae	9	9	146400	12	12	169200	8	8	143200	9	9	97000	6	6	161000	5	5	99600
Polygalaceae				1	1	1000												
Rhamnaceae	1	1	16	2	3	33	2	3	34	1	1	2	2	2	18	1	1	1
Rubiaceae				5	5	1403	1	1	2400				1	1	5			
Rutaceae	1	1	2	3	3	6	1	1	21	1	1	2	2	2	6	1	1	21
Salicaceae						1	1	1	39				1	1	1	1	1	12
Sapindaceae	1	1	3	1	1	33				1	1	2	1	1	9			

	Uninvaded (UI)						Lantan-invaded (LI)											
Sapotaceae	1	1	1	1	1	2							1	1	9			
Scrophulariaceae							1	2	10800									
Solanaceae				1	1	400	2	2	1264									
Spigeliaceae							1	1	1400				1	1	200			
Ulmaceae	1	1	1	1	1	1				1	1	1	1	1	1			
Verbenaceae	1	1	96	1	1	112	1	1	128	1	1	16176	1	1	17440	1	1	14512
Violaceae													1	1	400			
Vitaceae							1	1	48							1	1	256

The Shannon's index (H') ranged from 0.35–1.81, 0.41–2.00 and 0.46–2.12 in UI sites and from 0.51–1.61, 0.66–2.08 and 0.50–1.91 in LI sites, for saplings, juveniles and adults, respectively, and the values were significantly ($p < 0.05$) lower in LI sites than in UI sites (Figs. 3–7). For herbs the values ranged from 1.77–3.03 and 1.80–2.60 in UI and LI sites respectively. Significantly ($p < 0.05$) lower Shannon's index has been observed in LI than in UI sites. Simpson's dominance index (C_d) of saplings, juveniles and adult tree species ranged from 0.19–0.80, 0.18–0.76 and 0.14–0.83 in UI sites and 0.20–0.65, 0.16–0.64 and 0.21–0.76 in LI sites respectively, and the values were significantly ($p < 0.05$) lower in LI than UI sites (Figs. 3–7). In case of herbs, it ranged from 0.06–0.25 and 0.09–0.30 in UI and LI sites respectively. Whereas, the evenness index (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 highest evenness has been observed in LI than in UI sites. Herb evenness ranged from 0.33–0.71 and 0.33–0.76 in UI and LI sites, respectively and was significantly higher in LI sites than in UI sites (Figs. 3–7). The Margalef's index (R) of tree saplings, herbs and total plants reduced significantly ($p < 0.00$) in LI than UI sites (Figs. 3–7).

Impact on density and basal area

A significant impact of *Lantana* density (No. ha⁻¹) has been observed on the density (No. ha⁻¹) and basal area (m² ha⁻¹) of trees and herbaceous vegetation in LI than UI sites (Table 2). The density of tree saplings and juveniles decreased significantly ($p < 0.001$) with increase in *Lantana* density, whereas, the adult tree density did not show any significant trend (Figs. 2–6). The tree density of saplings and juveniles ranged from 4–308 and 4–100 in UI and 104–1336 and 132–732 in LI sites, respectively. The mean density of saplings and juveniles reduced significantly ($p < 0.001$) and was highest in UI (109 & 623) than LI (29 & 373) sites. The adult tree density ranged from 312–664 and 248–424 in UI and LI sites, with the mean of 456 and 331 respectively. The total tree density (saplings + juveniles and adults) also showed a significant ($p < 0.001$) declining trend in LI than UI sites. The total tree density in LI sites reduced significantly ($p < 0.05$) and ranged from 452–1116 and in UI sites from 528–1960, with the mean of 734 and 1118, respectively. The mean herb density declined significantly ($p < 0.001$) in LI sites than UI sites. The herb density ranged from 289000–640000 and 188000–373000 in UI and LI sites, with the mean of 451866 and 284466, respectively. In total a reduction of -53, -25, -16, -23, and -20% in density of saplings, juveniles, adults, herbs and total D respectively, has been observed in LI sites compared to UI sites, except shrubs & lianas density, which was having 76% higher density in LI than UI sites (Fig. 2).

The basal area of saplings and juveniles decreased significantly ($p < 0.001$) 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 ($p < 0.001$) in LI sites and ranged from 0.00–0.02 and 0.34–2.09 in LI sites, and 0.01–0.15 and 0.43–4.29 in UI sites, with the mean basal area of 0.05 and 1.89, and 0.01 and 1.21 respectively. The adult tree basal ranged from 14.5–30.3 and 11.5–23.4 in UI and LI sites with the mean of 19.7 and 14.7, respectively (Figs. 2–6). The total tree basal area reduced significantly ($p < 0.01$) in LI sites and ranged from 13.5–24.1 and in UI sites from 15.2–33.1, with the mean of 15.9 and 21.6, respectively. The mean herb basal area declined significantly ($p < 0.001$) in LI sites than in UI sites. The herb basal area ranged from 4.3–9.2 and 2.6–7.1 in UI and LI sites, with the mean of 6.7 and 4.8 respectively. In total a reduction of -67, -22, -15, -18, and -11% in basal area of saplings, juveniles, adults, herbs and total D respectively, has been observed in LI sites than UI sites, except shrubs & lianas, which are having 78% higher basal area in LI than UI sites (Fig. 2).

Impact on family composition

The number of species in a family varied from 1–17 and 1–13 in UI and LI sites respectively. Out of 141 species, 88 species from 35 families were found to be common in both UI and LI sites. Forty four species from 7 families and 10 species from 2 families were found only in UI and LI sites respectively. Fabaceae (17(UI) and 13(LI) species), Poaceae (12(UI) and 9(LI), 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 3).

Impact on diameter class distribution

Tree density decreased significantly ($p < 0.001$) with increase in diameter class in both UI and LI sites. The highest density of 51.8% was contributed by 3.1–10 cm size class and lowest of 0.7% density was contributed by > 50 cm size class in both UI and LI sites. Tree density of lower diameter class (< 3 DBH) was reduced by 57% in LI sites followed by 25, 23, 16, 13 and 10 % of 3.1–10, 30.1–40, 10.1–20, 20.1–30 and 40.1–50 DBH classes respectively (Fig. 8). In both LI and UI sites, the first three DBH classes (< 3–20 cm) contributed 81.8% of the total density, whereas, the other four DBH classes (> 20 cm) contributed 18.2% of the total density.

Impact on the soil properties

The values of soil bulk density (g cm^{-3}) and pH were significantly ($F = 12.96$, $p < 0.05$) lower in LI than in UI sites, whereas, soil moisture (%) was significantly ($F = 68.55$, $p < 0.001$) higher in LI than in UI sites (Fig. 9). The SOC and STN stocks were significantly ($F = 48.3$, $p < 0.001$; $F = 51.7$, $p < 0.001$) higher in LI than in UI sites (Fig. 9).

Correlation between *Lantana* densities with other different variables

The species richness of tree seedlings, juveniles and herbs showed a significant negative correlation ($r = -0.261$ to -0.720 , $p < 0.001$, Table 4) with *Lantana* density, whereas, a non-significant negative correlation was observed in SR of adult and total trees with *Lantana* densities. The density and basal area of tree seedlings, juveniles and herbs were significantly negatively correlated with *Lantana* density. Similarly, diversity indices (Simpson index, Shannon index, Fisher's alpha and Margalef's index) also showed a significant negative correlation with *Lantana* density, whereas, the evenness index of adult trees and herbs were significantly negatively correlated with *Lantana* density. The SOC, STN and M (%) showed a significant positive correlation, whereas, soil bulk density and pH showed a significant negative correlation with *Lantana* densities (Table 4).

Table 4
Correlations (r-values) between *Lantana* density and other predictable variables

Predictor variables	rvalue	Pvalue	Predictor variables	rvalue	Pvalue
Species richness			Density (No. of individuals ha⁻¹)		
Tree seedlings	-0.720	0.001	Tree seedlings	-0.867	0.001
Tree juveniles	-0.280	0.051	Tree juveniles	-0.312	0.023
Tree adults	-0.261	0.347	Tree adults	0.369	0.176
Total trees	-0.110	0.696	Total trees	-0.288	0.298
Herb	-0.385	0.044	Herb	-0.685	0.013
Basal area (m² ha⁻¹)			Shannon index (H')		
Tree seedlings	-0.887	0.001	Tree seedlings	-0.671	0.001
Tree juveniles	-0.168	0.045	Tree juveniles	-0.253	0.021
Tree adults	-0.047	0.869	Tree adults	-0.433	0.107
Total trees	-0.085	0.762	Total trees	-0.118	0.674
Herb	0.538	0.039	Herb	-0.037	0.053
Dominance index (D)			Simpson index (1-D)		
Tree seedlings	0.417	0.122	Tree seedlings	-0.663	0.001
Tree juveniles	0.153	0.041	Tree juveniles	-0.153	0.041
Tree adults	0.493	0.062	Tree adults	-0.493	0.062
Total trees	0.223	0.425	Total trees	-0.223	0.425
Herb	0.044	0.035	Herb	-0.044	0.035
Evenness index (E)			Fisher's alpha (α)		
Tree seedlings	0.033	0.908	Tree seedlings	-0.445	0.096
Tree juveniles	-0.054	0.848	Tree juveniles	-0.389	0.032
Tree adults	-0.472	0.076	Tree adults	-0.311	0.259
Total trees	-0.098	0.729	Total trees	-0.070	0.803
Herb	0.606	0.017	Herb	-0.028	0.024
Margalef's index (R)			Soil properties		
Tree seedlings	-0.613	0.015	SOC	0.890	0.043
Tree juveniles	-0.368	0.05	N	0.830	0.052
Tree adults	-0.291	0.292	pH	-0.987	0.002
Total trees	-0.072	0.799	M (%)	0.432	0.001
Herb	-0.024	0.035	BD	-0.513	0.051

Discussion

Comparing invaded and uninvaded sites aid us to measure the impact of invasive species on the native resident communities (Levine et al. 2003). In the present study, the LI sites had a significantly ($p < 0.05$) lower SR than the UI sites. Localities with *Lantana* invasion are known to have lower SR than uninvaded localities (Sharma and Raghubanshi 2010; Dobhal et al. 2011; Kumar et al. 2020). It is therefore evident that *Lantana* successfully establishes itself and competitively excludes the native 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 where some species are more easily excluded than the 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 & lianas and total species respectively in LI sites compared to UI sites. Increase in *Lantana* cover is known to cause pervasive losses in SR across multiple life forms (Gooden et al. 2009; Sharma and Raghubanshi 2010). The highest decline in SR was observed in the case of tree saplings, juveniles and herbs. This could be because *Lantana* produces a large number of 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 plant community (Kumar et al. 2020).

The values of Shannon index of diversity were lower in LI sites than UI sites for all the life forms and significantly in case of seedlings, juveniles and herbs. Shannon index is a measure of species richness of an ecosystem. *Lantana* invasion has often been associated with significant decreases in plant species richness, diversity and evenness in deciduous forest types (Sundaram and Hiremath 2012, Badalamenti et al. 2016). In the present study, the evenness index increased in LI sites for tree saplings, but decreased for the shrub and liana category. Changes in evenness of an ecosystem may impact the productivity, resistance to invasion and local plant extinction rates (Wilsey and Potvin 2000; Hejda et al. 2009). The impact of invasion largely depends on the degree of dominance (Pyšek and Pyšek 1995). Overall, the values of dominance index were higher in LI sites than UI sites. This is concurrent with the view that native plant community suppression often stems from the invasive species dominance in invaded habitats (Richardson et al. 1989). The increase in dominance is often linked to changes in species evenness and richness in invaded habitats (Hejda et al. 2009).

Fabaceae, Poaceae and Asteraceae were the most speciose families in the studied sites. Large families such as these are often the most well-represented and widely distributed in nature (Subashree et al. 2020). A family's dominance largely depends on its species' adaptability and the presence of favourable environmental conditions for pollination, seed dispersal and successful establishment (Panda et al. 2013). However, the number of families was slightly lower in LI sites (39) than UI sites (44). With unabated invasion of *Lantana* in the studied sites, the number of families would continue to decrease with decrease in species richness and local extinctions.

The species compositional changes induced by *Lantana* invasion are primarily driven by gradual changes in species density (Gooden et al. 2009). In this study, the density of tree seedling, juveniles and herbaceous vegetation reduced significantly ($p < 0.001$) with increase in *Lantana* density. Also, the frequency of occurrence of some tree species decreased in LI sites than UI sites. However, the density of shrub and lianas was greater in LI sites compared to UI sites, due to higher *L. camara* density. Overall, *Lantana* invasion suppresses the growth of trees by impacting the younger stages of development, viz. the sapling and juvenile stages, whereas the adult trees remained largely unaffected. This proves that *Lantana* is unlikely to displace tree individuals that have attained adult stage and the resistance/susceptibility of a particular species to invasion (Gentle and 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 ($p < 0.001$) lowered the basal area of tree saplings, juveniles and herbs in LI sites compared to UI sites. This might be due to the formation of a thick *Lantana* thickets that alters the microenvironment (such as light and temperature), inhibiting either germination or growth of other species (Sharma and Raghubanshi 2007), thus lowering the basal area of tree saplings, juveniles and herbs. Furthermore, at the ground level, there occurs accumulation of litter of *Lantana* comprising of fallen leaves and dry debris which also causes allelopathic suppression of growth and recruitment of seedlings, juveniles and herbs (Gentle and Duggin 1997). Basal area acts as an indicator of growth and biomass (Lewis et al. 2004). The changes in quantitative ecological parameters such as density, basal area and IVI by invasion of *Lantana* leads to alteration in plant assemblage patterns and forest structural characteristics (Rusterholz et al. 2018). This may eventually create demographic instability among the species and reduce diversity in the future (Sharma and Raghubanshi 2010).

Analysis of tree size class distributions reveals the population structure of a forest (Newbery and 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 behaviour, while their insufficient numbers denote poor regeneration (Saxena and Singh 1985). In this study, tree density declined significantly ($p < 0.001$) with increase in diameter class in LI sites than UI sites (Fig. 8). The highest contribution to the tree density was by lower diameter class of tree individuals (< 3–20 cm, 81.8%). This trend indicates that the tree species in the studied sites possess a good regenerative capacity. Even so, as observed in this study, 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 also known to displace natural scrub communities and prevent natural regeneration of some tree species (Ambika et al. 2003; Sharma and Raghubanshi 2006; Dobhal 2010). The recruitment of small-sized tree individuals into larger diameter classes has been known to be significantly impeded by *Lantana* invasion (Murali and Setty 2001; Sundaram and Hiremath 2012; Alemu and Terefe 2015). 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 soil bulk density and pH were significantly ($p < 0.001$) lower in LI sites than UI sites, soil moisture, soil organic carbon and soil total nitrogen showed a significant ($p < 0.001$) opposite trend. The observed trend is consistent with the findings of Niu et al. (2007), Dogra et al. (2009), Kumar et al. (2020). Invaded habitats experience changes in plant species composition and community structure and this alteration leads to changes in soil physico-chemical properties and nutrient dynamics (Hartman and McCarthy 2008; Rusterholz et al. 2018). The alteration in soil properties could be due to the release of allelochemicals by *Lantana*. The allelochemicals

released by the invasive plant species is known to alter the soil physical and chemical properties and regulate the biotic communities (Nardi et al. 2000). Very often, the altered soil properties provide favourable conditions for further invasion by *Lantana* and other invasive species (Niu et al. 2007). Soil moisture, soil organic carbon and total nitrogen are known to promote invasive species growth (Kumar et al. 2020). Therefore, invasion by *Lantana* not only affects the native resident plant community structure and composition, but also changes soil physio-chemical properties that may not be suitable for their growth.

In the present study, species richness, density, basal area, diversity indices (Shannon, Simpson, evenness, Fisher's alpha and Margalef) of tree seedlings, juveniles and herbs showed a significant negative correlation with *Lantana* densities (Table 4). Whereas, negative non-significant correlation with tree adults and total species (Table 4). Soil organic carbon (SOC), soil total nitrogen (STN) and soil moisture (M%) showed a significant positive correlation with *Lantana* densities, whereas, a significant negative correlation has been observed between pH and soil bulk density with *Lantana* density (Table 4). Similar findings have been recorded by Badalamenti et al. (2016) in Mediterranean ecosystems of Linosa island. In this study, *Lantana* density is found to be significantly positively correlated with its own biomass ($p \leq 0.01$), and shrub and liana density ($p \leq 0.01$), which could be attributed to its dominance in the shrub and liana category. Invasive plants are known to alter the soil pools and processes in ecosystems that they invade in by changing the quantity, quality, decomposition and mineralization (Ashton et al. 2005; Ruwanza and Shackleton 2016). *Lantana* density increases litter inputs and its chemical composition is also different from the native forest litter. The *Lantana* litter is rich in high SOC, N and soil moisture with low lignin content and favourable microclimate having faster decomposition rate and release of N. These alterations beneath the *Lantana* canopy significantly alter the SOC, total nitrogen pools and soil moisture in soils (Sharma and Raghubanshi 2009) and making the soil properties ideal for *Lantana* growth. The significantly higher M (%) content in LI sites than the UI sites could be due to the reason of soil water repellency due to increase in debris and organic matter from dead *Lantana* leaves, which are known to decompose slowly (Fan et al. 2010; Singh et al. 2014). *Lantana* produce a substantial quantity of litter (Singh et al. 2014) rich in allelopathic chemicals (El-Kenany and El-Darier 2013) which might react with organic matter and hydrophobic compounds to trigger repellency in the soils (Ruwanza et al. 2013). Soil bulk density and pH were significantly lower in LI sites than UI sites, which could be due to the higher litter content and its decomposition by micro-organisms. Similar results have been observed by Sharma and Raghubanshi (2009) in tropical dry deciduous forests of India. This could be the reason of *Lantana* success as an invasive species in these ecosystems. 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.

Conclusions

The present study revealed a significant negative impact of an alien invasive shrub, *Lantana* on species richness, density, basal area and diversity of vegetation of native plant communities. It is clear that *Lantana*-invaded sites comprise significantly lower richness, density and basal area than uninvaded sites. It not only impacts the vegetation of native communities, but also alters the soil properties, conclusively by favouring its growth. Furthermore, the alterations in vegetation structure, composition and soil properties could lead to changes in other tropical levels and change ecosystem functioning. Appropriate methods and long-term monitoring studies in permanent plots are needed for better understanding, management, and restoration as an effective and efficient conservation strategy for invaded landscapes in tropical forests.

Declarations

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Author's contributions

The study was conceptualized and designed by Parvaiz A Lone, Javid A Dar, Subashree K and Mohammed L Khan. Material preparation, field work, data collection and analysis were performed by Parvaiz A Lone, Javid A Dar and Subashree. The first draft of the manuscript was written by Parvaiz A Lone, Javid A Dar and Subashree providing review and comments by Mohammed L Khan. All authors's read and approved the submitted version of the manuscript.

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Conflicts of interest

No potential conflict of interest was reported by the authors

Availability of data and material

The data that support the findings of this study are available on request from the corresponding author

Abbreviations

LI	<i>Lantana</i> -invaded
UI	uninvaded

SR	species Richness
DBH	diameter at breast height
SOC	soil organic carbon
STN	soil total nitrogen
M	soil moisture
m	Meter
N	North
E	East
°C	degree Celsius
D	density
BA	basal area
IVI	Importance Value Index
APG	Angiosperm Phylogeny Group
GRIN	Germplasm Resources Information Network
C	carbon
cm	centimeters
H'	Shannon index
Cd	Simpson's dominance index
E	evenness
R	Margalef's index
ANOVA	analysis of variance

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Figures

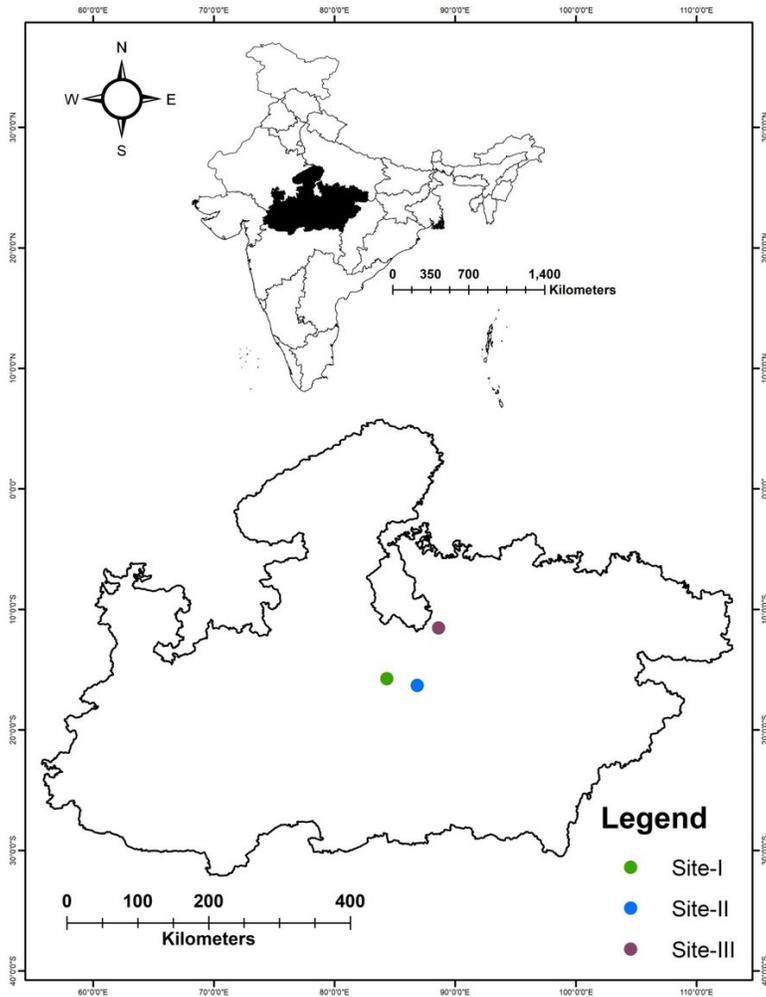


Figure 1
 Geographical location of three forests study sites of Madhya Pradesh, Central India. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

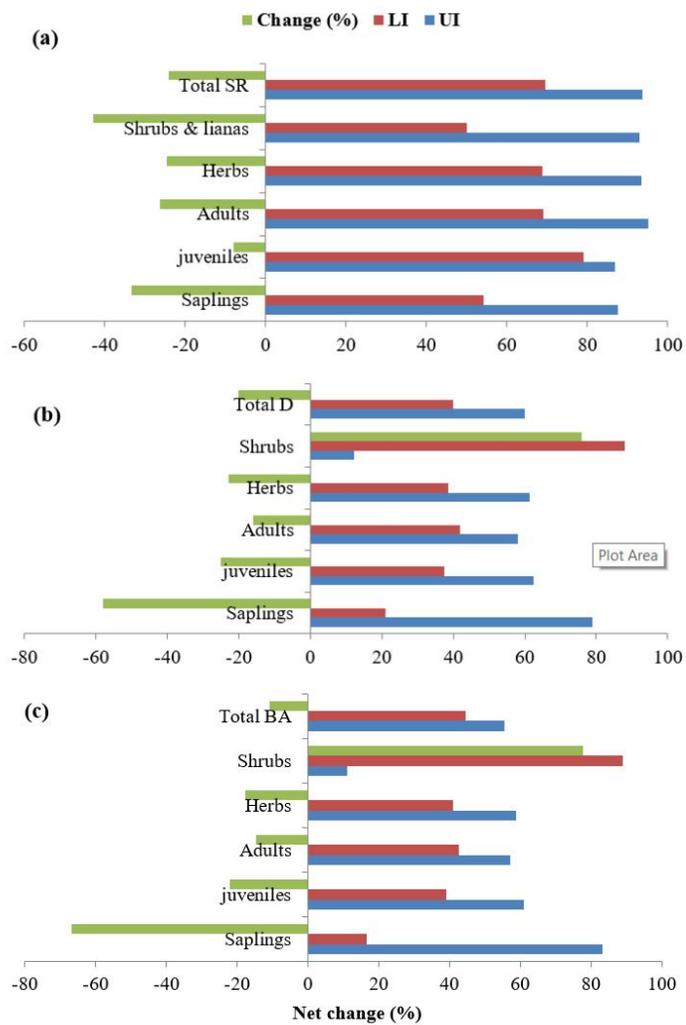


Figure 2
 Percent (%) change in a) species richness (SR), b) density (D) and c) basal area (BA) of saplings, juveniles, adults, herbs, shrubs & lianas and total SR, in uninvented (UI) and Lantana-invaded (LI) sites

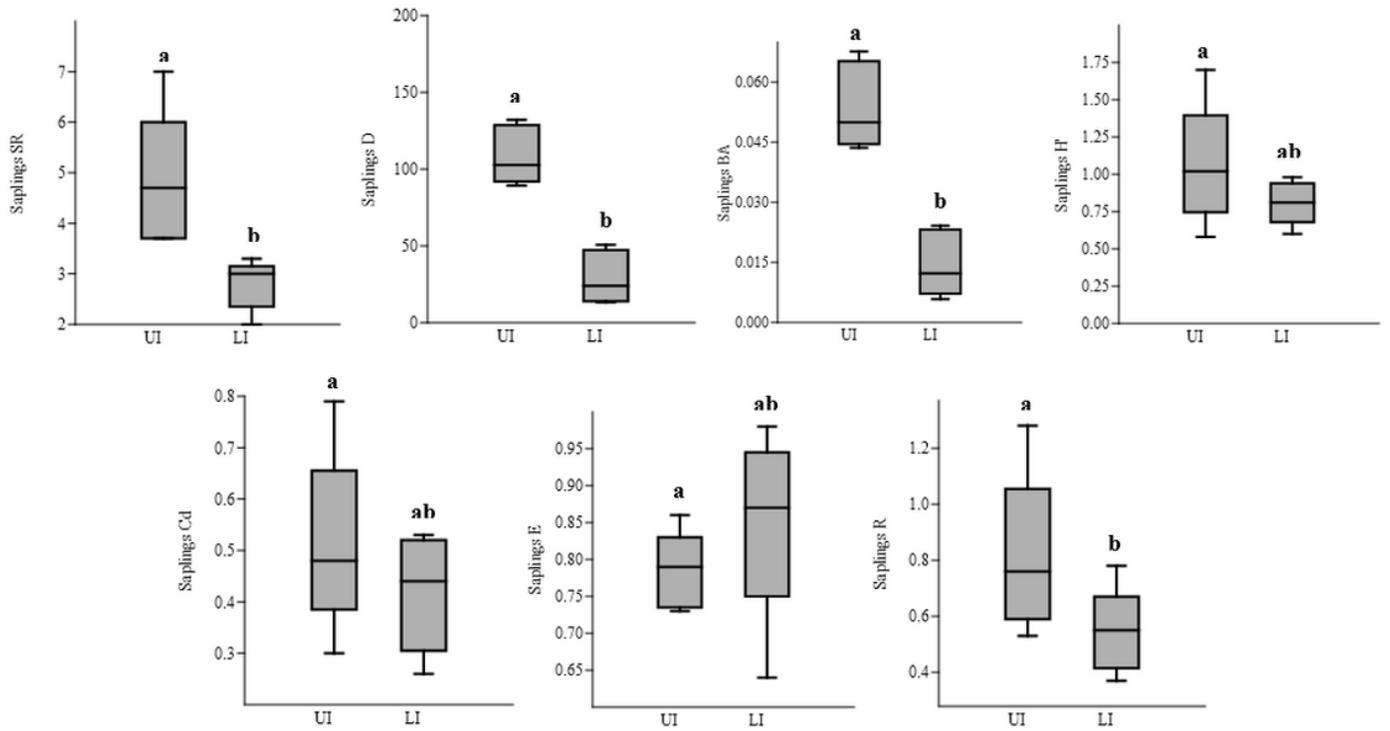


Figure 3
Species richness (SR; No. of species), density (D; stems ha⁻¹), basal area (BA; m² ha⁻¹), Shannon index (H'), Simpson index (Cd), evenness index (E) and Margalef's index (R) of tree seedlings in uninvaded (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at P<0.05

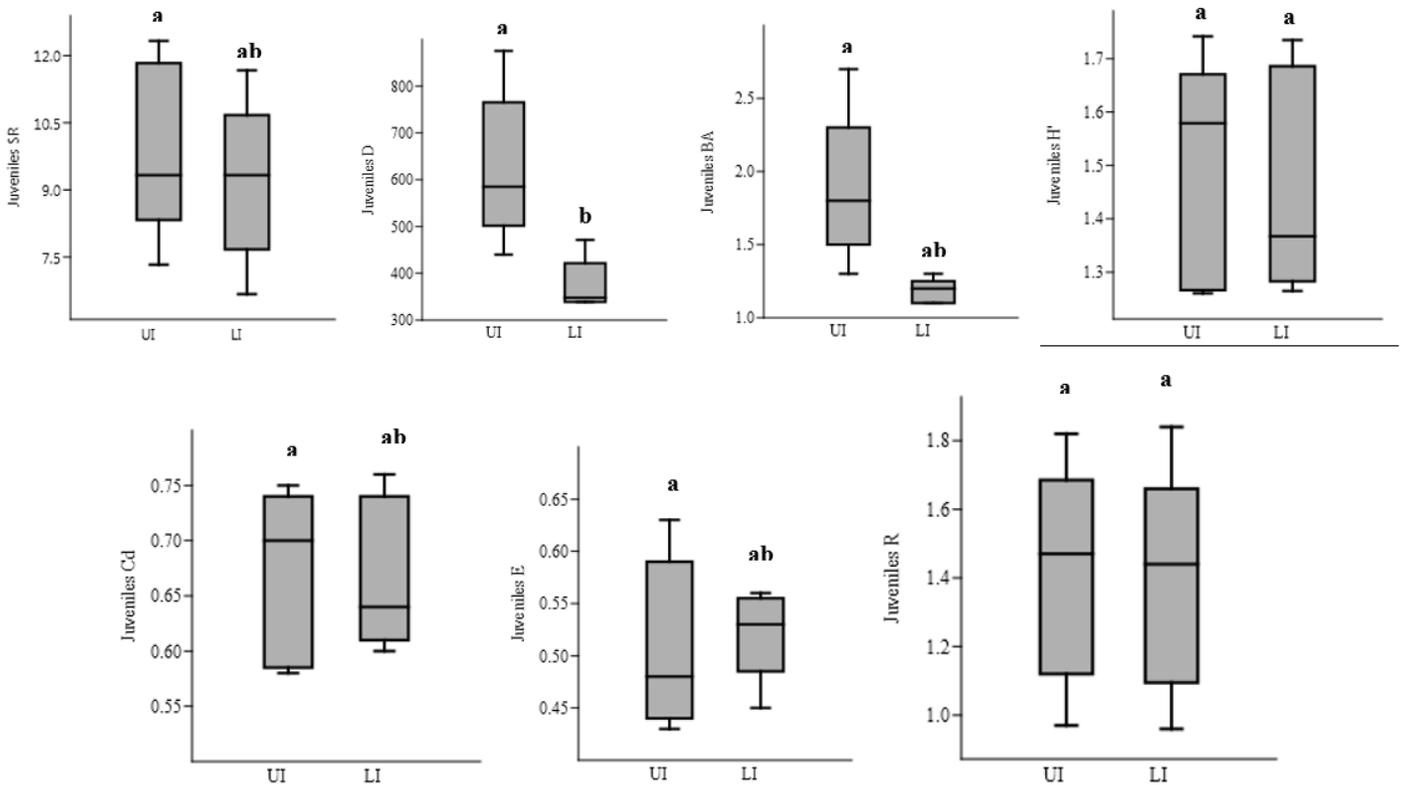


Figure 4
Species richness (SR; No. of species), density (D; stems ha⁻¹), basal area (BA; m² ha⁻¹), Shannon index (H'), Simpson index (Cd), evenness index (E) and Margalef's index (R) of tree juveniles in uninvaded (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at P<0.05

different at $P < 0.05$

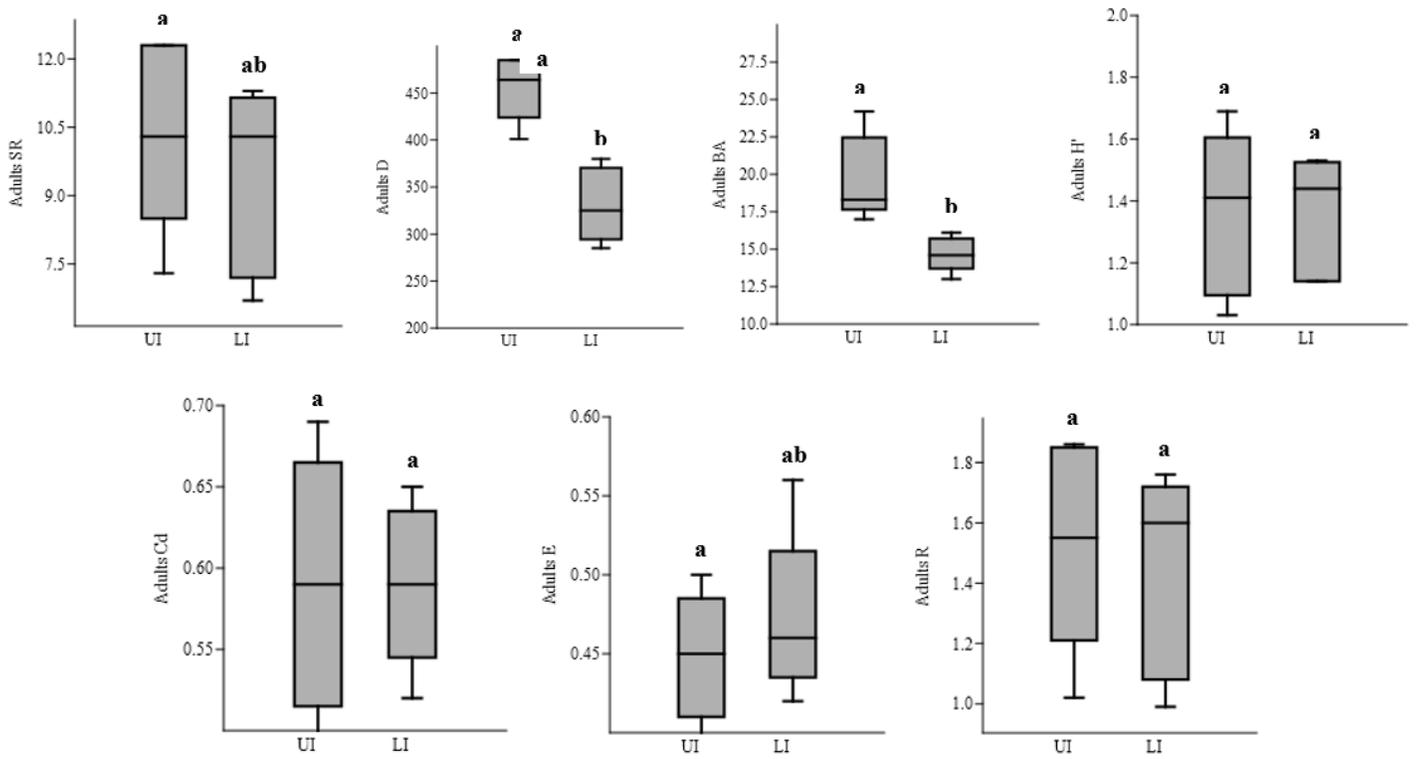


Figure 5

Species richness (SR; No. of species), density (D; stems ha⁻¹), basal area (BA; m² ha⁻¹), Shannon index (H'), Simpson index (Cd), evenness index (E) and Margalef's index (R) of tree adults in uninhabited (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at $P < 0.05$

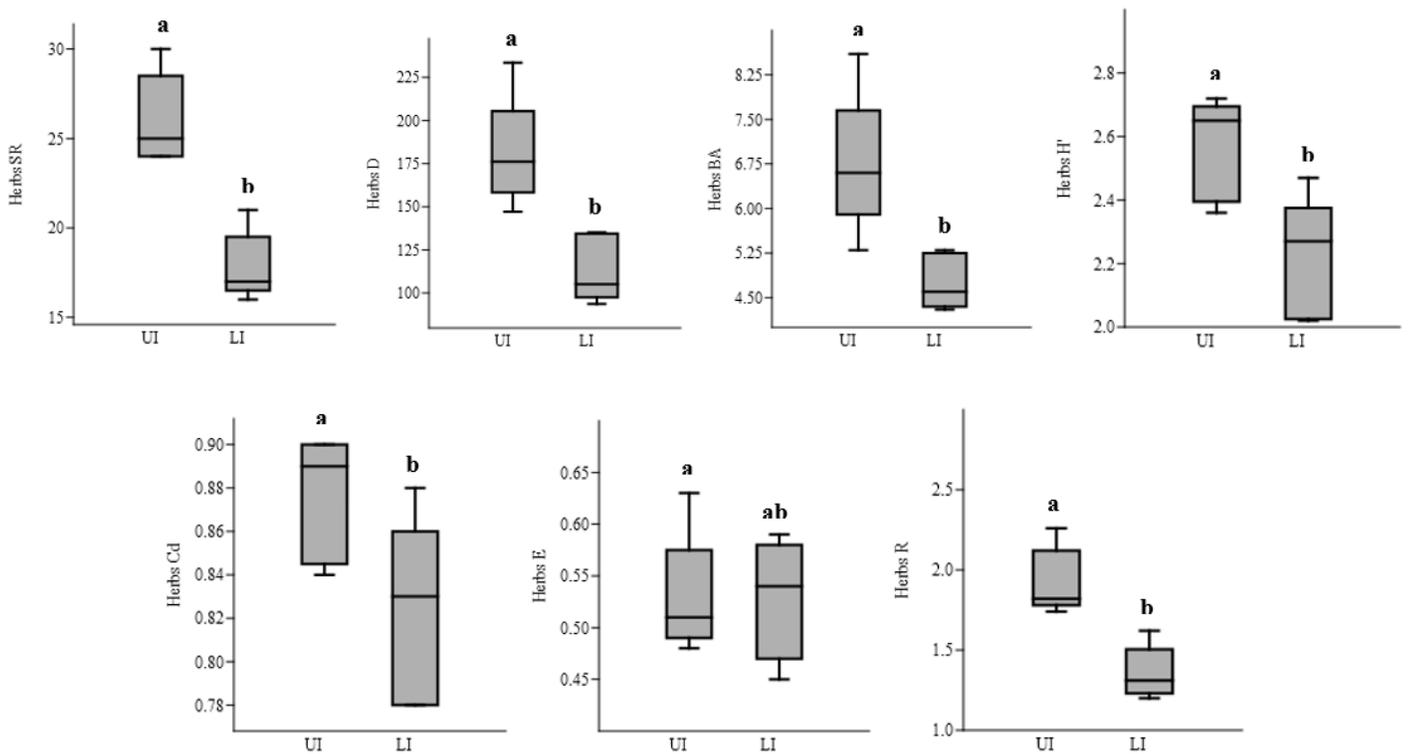


Figure 6

Species richness (SR; No. of species), density (D; stems ha⁻¹), basal area (BA; m² ha⁻¹), Shannon index (H'), Simpson index (Cd), evenness index (E) and Margalef's index (R) of herbs in uninvaded (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at P<0.05

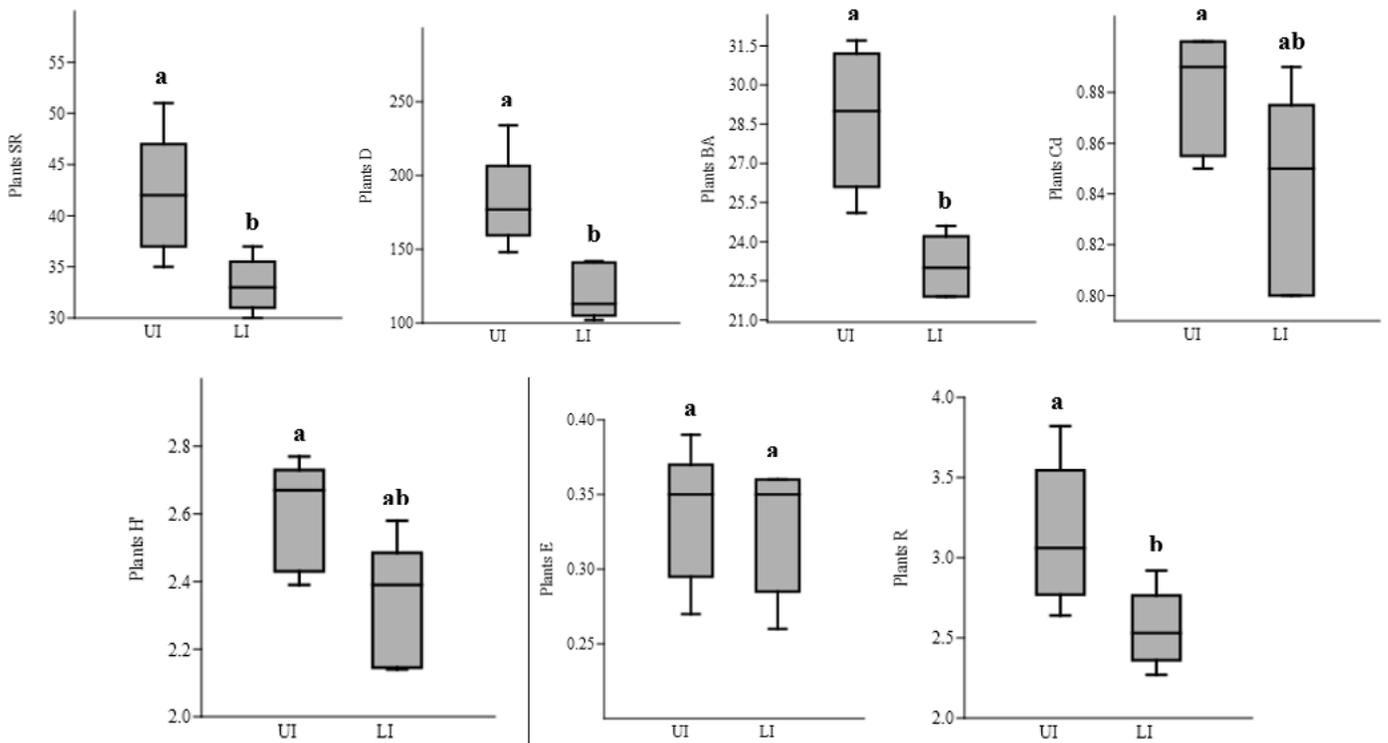


Figure 7

Species richness (SR; No. of species), density (D; stems ha⁻¹), basal area (BA; m² ha⁻¹), Shannon index (H'), Simpson index (Cd), evenness index (E) and Margalef's index (R) of total plants (trees, herbs and shrubs) in uninvaded (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at P<0.05

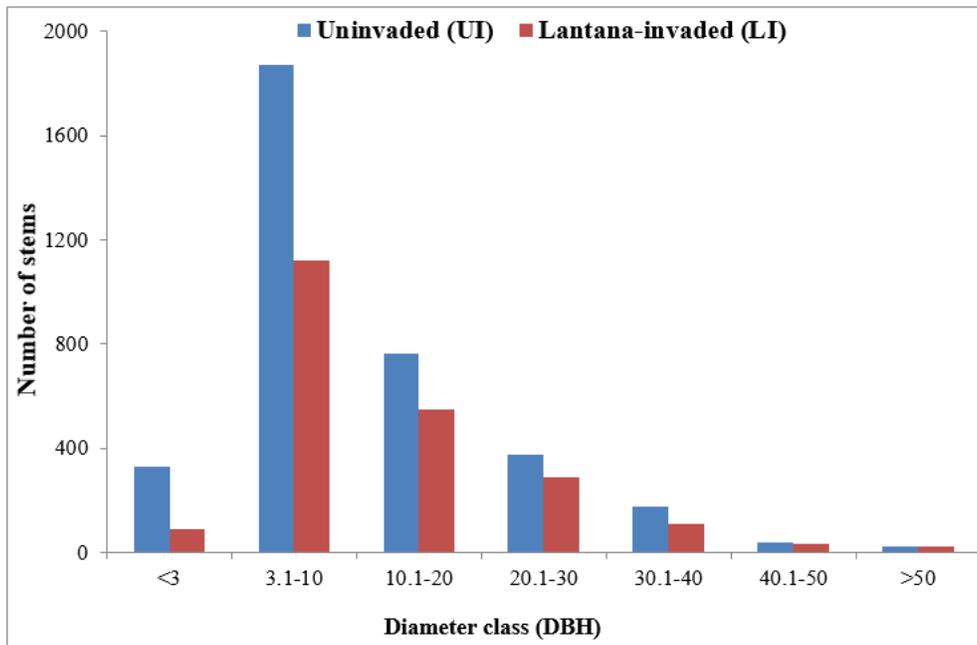


Figure 8

Diameter class-wise distribution of saplings (<3 cm), juveniles (>3.1-10 cm) and adult (>10 cm) trees in terms of stem density in uninvaded (UI) and Lantana-invaded (LI) sites

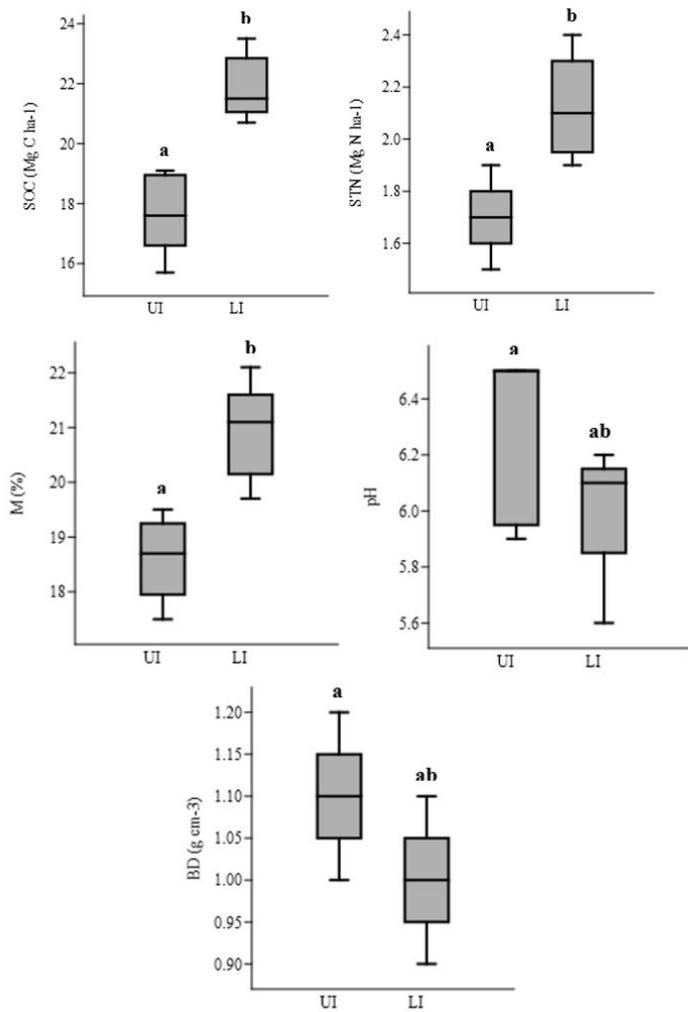


Figure 9
 Soil organic carbon (SOC; Mg C ha⁻¹), soil total nitrogen (STN; Mg C ha⁻¹), moisture (M; %), pH and bulk density (BD; g cm⁻³) in uninvaded (UI) and Lantana-invaded (LI) sites. Data are presented as the mean value, different letters are significantly different at P<0.05

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