Plant Ecology
https://doi.org/10.1007/s11258-024-01441-6

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Assessing the influence of invasion of *Lantana camara* on vegetation attributes and soil properties across varied disturbance gradients in semi-arid forests of Aravali hills, Delhi

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Received: 16 March 2024 / Accepted: 15 June 2024

Abstract
This study highlights the coupling effect of disturbance and *Lantana camara* invasion on vegetation and soil properties in the least disturbed (LD), moderately disturbed (MD) and highly disturbed (HD) sites in the semi-arid region of Aravalli Mountain, South Delhi. A total of 60 quadrats of 10 m × 10 m were laid for tree species and 5 m × 5 m for shrub species in the LD, MD and HD sites for phytosociological study. Soil samples were collected at three places: areas occupied by *Lantana camara* (LC) and *Adhatoda vasica* (AV), as well as areas of bare soil (no vegetation) at two different depths: the upper layer (0–10 cm) and the lower layer (10–20 cm). Results showed higher tree diversity in the LD site, whereas shrub diversity was high in HD site. The relative density (RD) of invasive *L. camara* and soil properties was maximum in MD (61.5%) and minimum (55.5%) in HD site, however low soil nutrients in HD site may be due to the lower RD of LC. Statistical analysis showed significant ($p < 0.05$) high soil moisture, soil organic carbon (SOC), microbial biomass carbon (MBC) and nitrogen (MBN) in MD site. SOC, TN, MBC and MBN were higher under LC-occupied regions compared to AV in LD and MD sites. In HD site, nutrient content was higher under AV region, reflecting that in nutrient-deficit soil, native species adapt and resist the invasion of LC. However, among the different biotic and abiotic factors, disturbance is one of the major drivers that promotes plant invasion.

Keywords Disturbance · Invasion · *Lantana camara* · Semi-arid · Soil microbial biomass

Introduction

In the present changing climate, plant invasion is a major concern in the scientific community. Plant invasion causes loss in species diversity, and changes soil processes, consequently affecting livelihood and ecosystem health (Mungi et al. 2020; Kumar et al. 2021). Disturbance is one of the major factors in the facilitation of plant invasion (Catford et al. 2012; Mondal et al. 2024). An increasing rate of disturbances like browsing, grazing, and trampling tends to create empty niches which may promote biological invasion by providing favourable conditions (Hobbs and Huenneke 1992; Alpert and Maron 2000; Jauni et al. 2015). Disturbance alters the physical environment and resource availability such as light and nutrients and also reduces the competitive out-turn of the native vegetation, which can benefit the invader species (Davis et al. 2000; Orbán et al. 2021). Additionally, plant invasions are affected by the species type as well as the degree of disturbance (Mallon et al. 2015; Aththanayaka et al. 2023). The success of plant invasion is attributed to its potential to modify the soil's physical, chemical and biological properties (Si et al. 2013; Castro-Díez et al. 2016; Ahmad et al. 2019). Plant invasion can also drive the soil hydrological cycle (Ehrenfeld 2003; Wilgen et al. 2020), soil pH (Herr et al. 2007; Lazzaro et al. 2014), and soil nutrient cycle (Kumar et al. 2020), litter dynamics (Mun and Lee 2020), carbon and nitrogen mineralization rates (Srivastava and Raghubanshi 2021; Nasto et al. 2022). These modifications in the soil system can promote positive plant-soil feedback for the alien species which ultimately escalates invasion (de la Peña

Communicated by Anna Corli.

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et al. 2010; Suding et al. 2013). Thus, predicting how diverse disturbance regimes could affect invasion outcomes is necessary for developing restoration strategies and effective ecological management (Poland et al. 2021).

Among the various invasive species, *Lantana camara* is one such invasive species that has caused global-scale problems and is considered to be among the world's 100 worst invasive species, as recognized by the Invasive Species Specialist Group (IUCN, 2001). *Lantana camara* L., commonly known as lantana belonging to the Verbenaceae family is native to Tropical America and is spread over more than 60 countries (Kato-Noguchi and Kurniadie 2021). In India, the flowering shrub lantana is expanding rapidly and threatens about 44% of the total Indian forest cover, and invades warm, humid and disturbed areas which are mainly caused by anthropogenic activities (Mungi et al. 2020). Numerous research have been carried out in the Indian Himalayan Region (Dobhal et al. 2010; Mandal and Joshi 2015; Kumar et al. 2021; Joshi et al. 2024), Western and Eastern ghats (Balaguru et al. 2016; Kishore et al. 2024), semi-arid and arid regions (Ramaswami et al. 2017; Kalra et al. 2023) focussing on lantana distribution, its impacts on native communities, soil properties, plant traits etc. However, very few studies have reported the influence of disturbance gradients on the distribution of lantana and soil properties particularly in semi-arid environments. In the present study, we tried to investigate the distribution pattern of native (*Adhatoda vasica)* and invasive (*Lantana camara*) shrub species across the different disturbance gradients.

The Delhi Ridge Forest exists in the semi-arid regions and is dominated by invasive species such as *Prosopis juliflora*, *Lantana camara*, *Parthenium hysterophorus*, *Ageratum conyzoides* etc. Amongst the above-mentioned species, Lantana is one such invasive alien plant species that is of major concern, and it has widely spread in forests (mostly disturbed forests), roadside and agricultural lands (Love et al. 2009; Negi et al. 2019), and thus was selected for this research work. Previously, it was reported that the invasion of lantana showed both, positive and negative impacts on species composition (Sharma and Raghubanshi 2011). In Delhi Ridge, many shrub species are found along with lantana such as *Adhatoda vasica*, *Abutilon indicum* etc. *Adhatoda vasica* (Nees) is an evergreen shrub native to Asia and it holds great importance in Ayurvedic and Unani medicine for the treatment of various diseases (Claeson et al. 2000). This species was found across all the disturbance gradients alongside lantana and was thus chosen for a comparative study between native and invasive shrub. A study conducted on Delhi Ridge (Naudiyal et al. 2017) found that grazing, trampling and wood cutting are the major disturbances on the ridge and it has a significant impact on the vegetation. Therefore, the present study tried to highlight a comparative study of both native and invasive shrub species along the disturbance gradients. We analyzed the impact of lantana on species density, diversity, and soil physical and biochemical properties across varying disturbance gradients in the semi-arid forest ecosystem. Here, we hypothesize that with the increasing disturbance intensity, there will be a change in both vegetation structure and soil properties. To test the above hypothesis, we framed the following objectives. (1) to assess variation in species density, diversity and basal area of lantana and adhatoda in the least disturbed (LD), moderately disturbed (MD) and highly disturbed (HD) sites of Aravalli hills. (2) to analyze variations in soil physical and biochemical properties across disturbance gradients in *Lantana camara* (LC)*, Adhatoda vasica* (AV) occupied regions and bare soil (BS). (3) to determine the combined effects of disturbance and plant invasion on soil properties across the selected sites.

Methodology

Study area

The present study was conducted in the South Delhi ridge (Fig.1), of the Aravalli Mountain range, the oldest mountain range which stretches about 692 km from Gujarat to Delhi. The climate is specified by hot summer (April to June), humid monsoon (July to September), and dry and cool winter (November to January). As per the Koppen classification, the climate of the Delhi region is humid subtropical (Cwa) to semi-arid (BSh) types (Pramanik and Punia 2020). The semi-arid region of Delhi forests belongs to the tropical forest type, and subtype tropical thorn forest (6B/C) (Champion and Seth 1968). The summer and winter seasons are characterized by extreme weather conditions. The study site receives maximum rainfall in the monsoon season. In the study area, the vegetation is mainly dominated by middle-story thorny trees due to their sparse distribution.

The major rocks are Quartzite, Sandstone and soil types are mainly sandy loam varying from sandy loam to clay loam (Tripathi and Rajamani 1999). The vegetation of Delhi comprises the thorny scrub found in arid and semi-arid regions. The dominant tree species in the region are *Acacia nilotica*, *A. leucophloea*, *A. catechu*, *Cassia fistula*, *Zizyphus* sp., *Anogeissus pendula*, *Bauhinia variegata*, *Prosopis juliflora* etc. The dominant shrub species are *Lantana camara*, *Capparis sepiaria*, *Bougainvillea spectabilis*, *Grewia tenax*, etc. (Kushwaha et al. 2014; Gaury and Devi 2017) .

Site selection and vegetation analysis

The study area was selected based on a reconnaissance survey conducted in October 2018. We considered

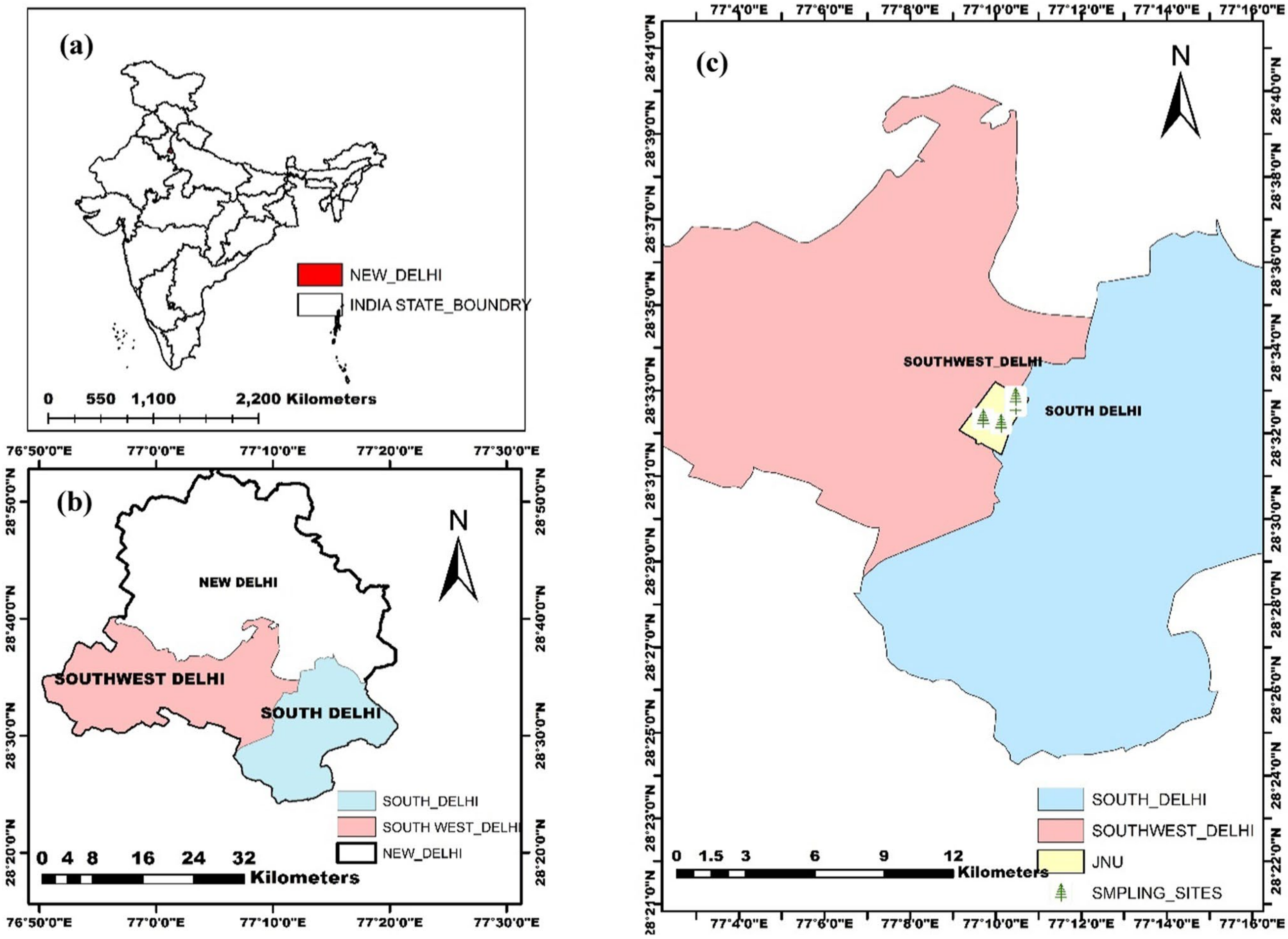

Fig. 1 Location of the selected research sites (**c**, presented in yellow colour) in the ridge region of southwest Delhi (**b**), India (**a**)

disturbance as a major gradient between the sites, and among the major disturbance factors, the presence of stumps or tree cuts, canopy cover, ground cover and human interventions were considered. The cut stumps of tree species were counted and measured at each site. Disturbance index (DI) was calculated as the basal area of cut trees measured at the ground level expressed as the fraction of the total basal area of all trees including felled ones by following Borah et al. 2014. Canopy cover was measured using a spherical densiometer, and the evidence of human activities such as trampling, littering and tracks of wild animals were observed. Following Rao et al. 1990, study sites were categorized based on the DI (%) values as: (a). HD site (DI > 40%, having canopy cover less than 40% and tree stump cut 19.7% and signs of lopping and grazing were also high.), (b). MD site (DI 20–40 % with the canopy cover of 40–60%, tree stump cut was 11.19% and signs of lopping and grazing were present), (c). LD site (DI up to 20%, having canopy cover of more than 60%, cut tree stumps was 2.62 % and some grazing signs were present).

The Detailed descriptions of the study sites are shown in Table 1.

In November 2018, following quadrat methods, we laid 60 plots in all sites, 10 quadrats of 10 m x 10 m were laid for tree species and 10 quadrats of 5 m × 5 m for shrub species were performed in each site for the phytosociological analysis (Dutta and Devi 2013). Individuals were identified at their species level. The phytosociological analysis was done to quantify density, frequency, and abundance (Curtis and McIntosh 1950). The basal area of tree species (≥ 10 cm dbh) was analyzed by measuring the circumference of the tree stem at breast height (CBH) at 1.37 m above ground level. For the shrub species, the basal area was analyzed using vernier calliper by measuring the girth of each tiller at 8 cm above the ground. To calculate species diversity, we calculated the Shannon–Wiener Diversity Index (H`) following Shannon and Weaver (1963), Simpson's Concentration of dominance (Cd) as described by (Simpson 1949), Species evenness (SE) based on Pielou (1966) and Species Richness (SR) using Margalef (1958).

Table 1 Categorization of study sites based on visible signs of disturbance

Sites	LD	MD	HD
Latitude	28°31′ 0″ N	28°32′ 0 ″ N	28°32′ 0″ N
Longitude	77°9′ 0″ E	77°10′ 0″ E	77°10′ 0″ E
Canopy cover	> 60%	40–60%	< 40%
Ground cover	~ 70%	~ 60%	> 50%
Number of cuts and stump	2.62%	11.19%	19.17%
Signs of human interventions observed	Grazing	Stump, lopping, grazing and trampling	Stump, lopping, trampling and grazing

LD Least Disturbed, *MD* Moderately Disturbed, *HD* Highly Disturbed

Soil sampling and analysis

In each site, we identified three regions to collect soil samples; firstly, *Lantana camara* occupied (invasive shrub), secondly *Adhatoda vasica* (native shrub) occupied, and thirdly, open space (called bare soil (BS) where no vegetation was present. Soil corer having a diameter of 5 cm was used for soil collection. All soil samples were collected in triplicate at two soil depths viz. upper layer (0–10 cm) and lower layer (10–20 cm). Collected cored soil samples were sieved with a mesh size of 2 mm and then air-dried to analyze physicochemical properties. Soil moisture content was measured by oven-drying fresh soil at 105 °C to constant weight. Soil pH and electrical conductivity (EC) were measured using digital pH and EC meter. Soil bulk density (BD) was determined as dry soil mass per unit volume (Okalebo et al. 2002). Soil organic carbon (SOC) was estimated following the modified Walkley and Black method (Walkley and Black 1934). Soil total nitrogen (TN) was estimated using a micro-Kjeldahl digestion and distillation unit (Jackson 1958). Soil microbial biomass carbon (MBC) and biomass nitrogen (MBN) were measured using chloroform fumigation and extraction method (Brookes et al. 1986; Vance et al. 1987).

Statistical analysis

Soil data normality was assessed based on Shapiro–Wilk's test and homogeneity of variance was tested by Levene's test. Vegetation parameters were determined using the vegan package. Two-way analysis of variance (ANOVA) was performed to test the significant differences among the disturbance gradients (HD, MD and LD) and among the LCO, AVO and BS, followed by Tukey's post hoc test was conducted to analyze pairwise comparisons between each site. Further, soil properties were checked for correlation using the ggpairs package. Principal component analysis (PCA) was used to evaluate the proportion of variance explained by disturbance, invasion and their interaction with soil properties using the ggfortify package. We also performed variance decomposition analysis to quantify the relative contribution of disturbance, species type, soil depth and vegetation parameters that shape the soil properties in the region using the varpart function of the vegan package. All statistical analyses were conducted using R version 3.5.0 (R Core Team, 2018).

Results

Influence of *Lantana camara* invasion on species density, diversity and basal area along disturbance gradients

We found a total of 10 tree species and 6 shrub species in the selected sites. Tree density and basal area decreased from LD to HD sites (Table S1). Tree density was found higher in LD (510 ind ha^{-1}) followed by MD (440 ind ha^{-1}) and minimum in HD site (230 ind ha^{-1}). Similar to tree density, basal area was higher in LD (48.11 m^2 ha^{-1}) followed by MD (43.82 m^2 ha^{-1}) and minimum in HD (33.65 m^2 ha^{-1}). One-way ANOVA showed significant variation in tree density (F = 2.5, $p < 0.05$) and tree basal area (F = 3.81, $p < 0.05$) with the disturbance gradient. Shannon-Weiner diversity (H`) and species richness (SR) for the tree layer were found to be maximum for the LD site and least for the HD site, while the concentration of dominance was observed maximum for the HD site (Fig. 2). Unlike the tree layer, total shrub density varied from 140 to 540 ind ha^{-1}, and was found maximum in HD followed by LD and MD sites (Fig. 3). Across the disturbance gradients, the contribution of invasive species, *L. camara* to the total shrub density was found highest in the MD site (80 ind ha^{-1}) i.e., around 61%. Whereas, the native species, *A. vasica* attributed maximum in LD (90 ind ha^{-1}) i.e., around 19% and minimum in HD site (70 ind ha^{-1}) i.e., around 13% (Table S2). Shrub basal area was found maximum in the LD site (8.89 m^2 ha^{-1}) followed by HD (6.69 m^2 ha^{-1}) and minimum in MD sites (4.44 m^2 ha^{-1}). One-way ANOVA showed significant

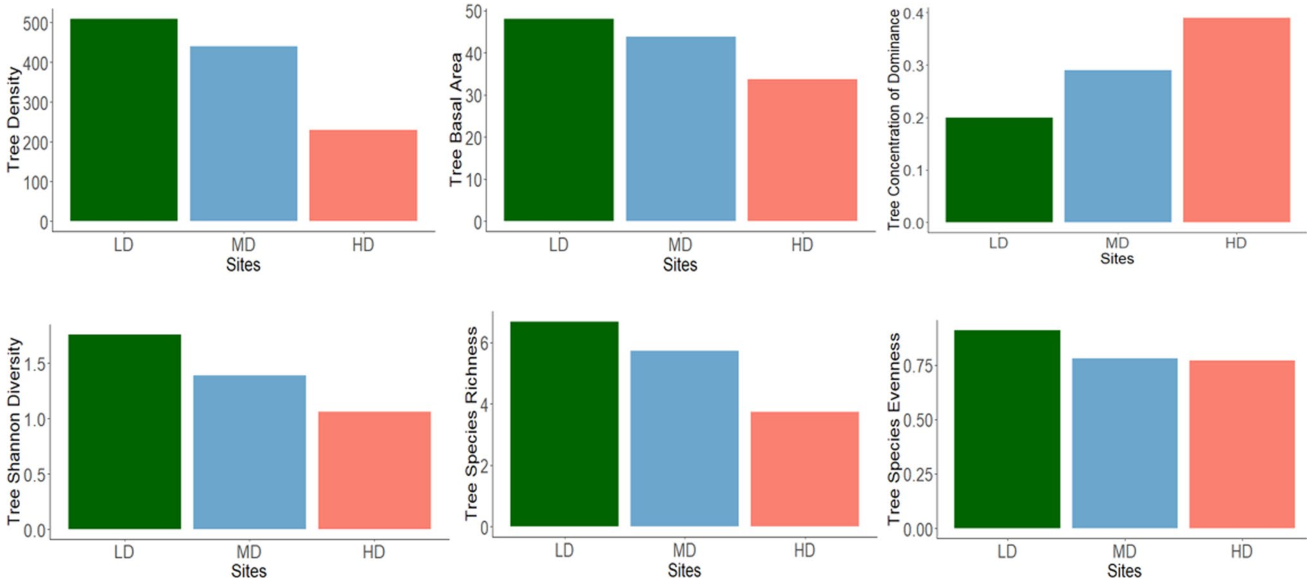

Fig. 2 Variation in Basal Area (m^2 ha^{-1}), Density (ind ha^{-1}), Concentration of Dominance, Species Richness (SR), and Diversity indices (H`:Shannon diversity and Species Evenness) with increasing disturbance intensity (*LD* Least Disturbed, *MD* Moderately Disturbed, *HD* Highly Disturbed) for tree species

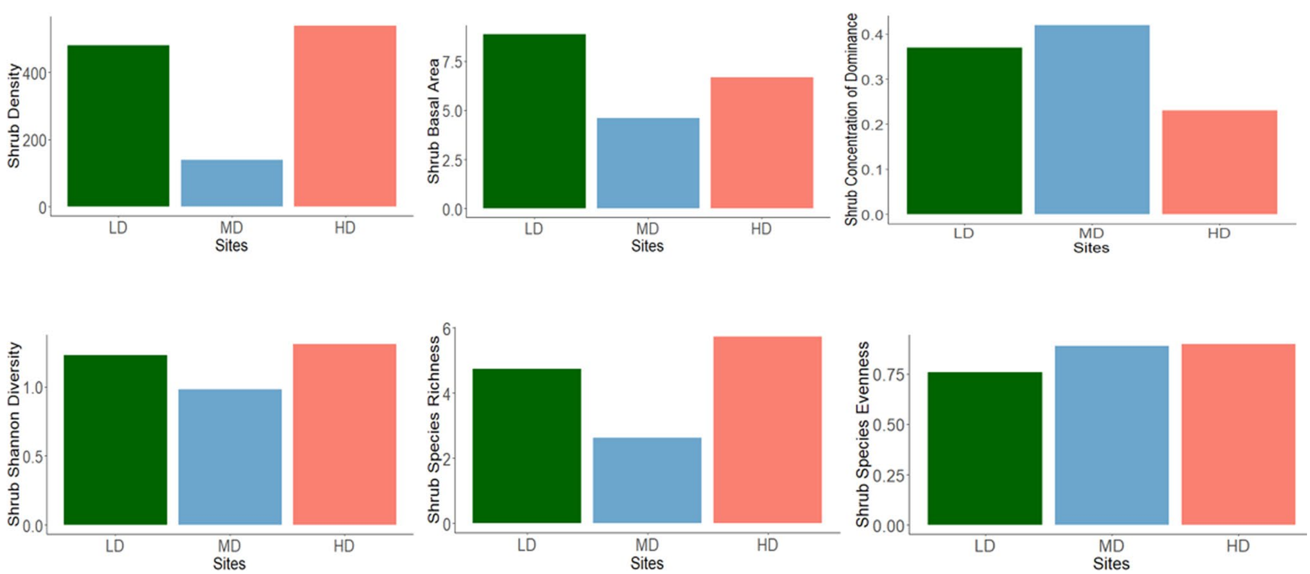

Fig. 3 Variation in Basal Area (m^2 ha^{-1}), Density (ind ha^{-1}), Concentration of Dominance, Species Richness (SR), and Diversity indices (H`:Shannon diversity and Species Evenness) with increasing disturbance intensity (*LD* Least Disturbed, *MD* Moderately Disturbed, *HD* Highly Disturbed) for shrub species

variation in shrub density ($F = 6.35$, $p < 0.05$) and shrub basal area ($F = 1.56$, $p < 0.05$) with varying disturbance intensity.

Soil physical and bio-chemical properties in LD, MD and HD sites

Statistical analysis of soil properties (LC, AV and bare soil sites) along the disturbance gradients (LD, MD and HD) altogether forming nine sites is represented in Fig. 4). Across the disturbed sites, the soil moisture content ranged from 9.93 ± 0.04% to 25.63 ± 4.26% in

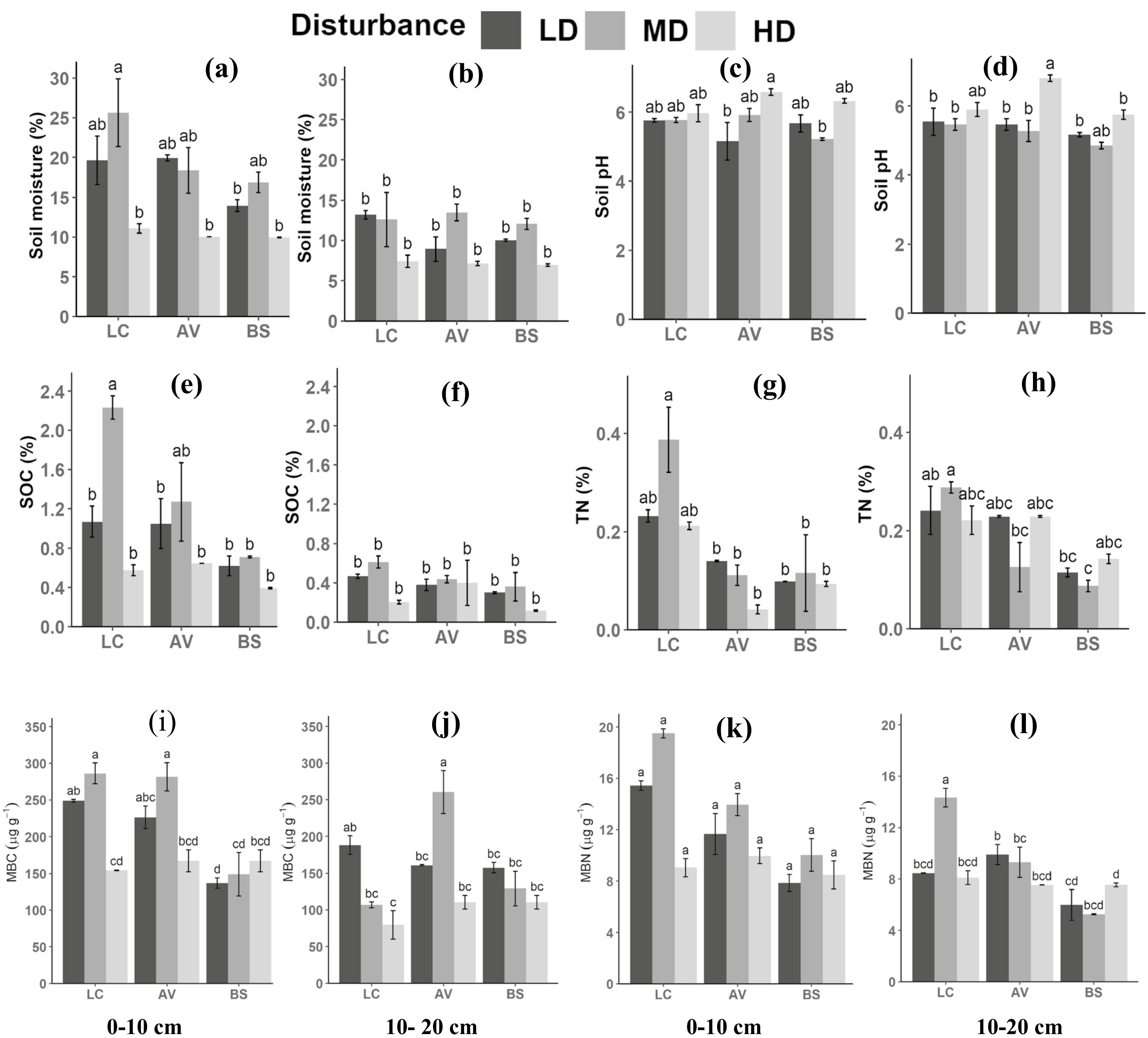

Fig. 4 Bar plot showing soil physical and biochemical soil properties in the least disturbed (LD), moderately disturbed (MD) and highly disturbed (HD) sites (n = 3 ± SE). *SOC* = soil organic carbon, *TN* = soil total nitrogen, *MBC* = soil microbial biomass carbon, *MBN* = soil microbial biomass nitrogen. Small letter (abcd) showing significant ($p < 0.05$) difference among LD, MD and HD in *Lantana camara* (LC) and *Adhatoda vasica* (AV) occupied regions, and in bare soil

the surface layer (0–10 cm). In comparison to the HD site, soil moisture content was significantly ($p < 0.05$) higher in the MD site. However, in lower depths (10–20 cm), soil moisture content was almost similar in all three disturbances. Soil pH ranged from 4.84 ± 0.09 to 6.803 ± 0.09 across the disturbance gradient and was significantly higher in the HD site. Soil pH was higher in the *L. camara*-occupied soil than in the *A. vasica*-occupied (Table 2). SOC and TN ranged from 0.39 ± 0.00 to 2.23 ± 0.11 and 0.08 ± 0.01 to 0.28 ± 0.01, respectively across the disturbance gradient in the surface soil layer (Table 2 and 3). In the LC-occupied region, SOC and TN were found to be significantly higher in MD compared to LD and HD in the surface soil layer (Fig. 3, 4). Soil microbial carbon ranged from 131.62 ± 6.99 µg g-1 to 286.22 ± 14.23 µg g^{-1} across the disturbances and was found significantly higher in the MD site compared to LD and HD sites in the surface soil layer in both *L. camara* and *A. vasica* occupied regions (Fig. 4i, and Table 2). In bare soil, MBC did not differ significantly with disturbance gradient in both the surface and lower layer

Table 2 Values of soil physical and biochemical parameters in *Lantana camara* and *Adhatoda vasica* occupied regions in LD, MD and HD sites

Attributes		LD			MD			HD		
Soil Parameters	Depth (cm)	LCO	AVO	BS	LCO	AVO	BS	LCO	AVO	BS
Moisture	0–10	19.66 ± 3.03	19.93 ± 0.37	13.95 ± 0.75	25.63 ± 4.26	18.37 ± 2.86	16.87 ± 1.25	11.08 ± 0.58	10.04 ± 0.00	9.93 ± 0.04
	10–20	13.20 ± 0.52	8.94 ± 1.52	10.03 ± 0.14	12.61 ± 3.37	13.50 ± 1.04	12.07 ± 0.70	7.41 ± 0.76	7.15 ± 0.26	6.95 ± 0.14
pH	0–10	5.76 ± 0.05	5.15 ± 0.54	5.67 ± 0.25	5.77 ± 0.07	5.92 ± 0.19	5.21 ± 0.03	5.96 ± 0.24	6.58 ± 0.09	6.32 ± 0.07
	10–20	5.54 ± 0.39	5.46 ± 0.17	5.16 ± 0.06	5.46 ± 0.17	5.27 ± 0.30	4.84 ± 0.09	5.90 ± 0.2	6.80 ± 0.09	5.74 ± 0.13
BD	0–10	0.95 ± 0.04	0.83 ± 0.05	1.06 ± 0.04	0.92 ± 0.02	1.00 ± 0.07	1.27 ± 0.06	1.47 ± 0.07	1.32 ± 0.02	1.63 ± 0.13
	10–20	0.96 ± 0.03	0.98 ± 0.00	1.14 ± 0.05	0.97 ± 0.02	1.14 ± 0.15	1.18 ± 0.15	1.35 ± 0.02	1.34 ± 0.03	1.68 ± 0.01
EC	0–10	227.9 ± 38.1	220.5 ± 13.5	185.05 ± 0.05	233.5 ± 14.5	174.8 ± 79.2	191.9 ± 41.1	256.5 ± 3.5	271.5 ± 12.5	265.5 ± 16.5
	10–20	171.6 ± 23.15	183.1 ± 0.4	163.25 ± 15.85	147.15 ± 18.95	179.95 ± 12.15	166.4 ± 22.8	178.5 ± 13.1	203.5 ± 20.5	222.5 ± 9.5
SOC (%)	0–10	1.06 ± 0.15	1.04 ± 0.25	0.61 ± 0.09	2.23 ± 0.11	1.27 ± 0.39	0.71 ± 0.01	0.57 ± 0.05	0.64 ± 0.00	0.39 ± 0.00
	10–20	0.46 ± 0.02	0.37 ± 0.05	0.30 ± 0.00	0.61 ± 0.06	0.43 ± 0.03	0.35 ± 0.14	0.20 ± 0.02	0.39 ± 0.22	0.11 ± 0.00
TN (%)	0–10	0.24 ± 0.04	0.22 ± 0.00	0.11 ± 0.01	0.28 ± 0.01	0.12 ± 0.05	0.08 ± 0.01	0.22 ± 0.02	0.22 ± 0.00	0.14 ± 0.01
	10–20	0.23 ± 0.01	0.14 ± 0.00	0.09 ± 0.00	0.38 ± 0.06	0.11 ± 0.02	0.11 ± 0.07	0.21 ± 0.00	0.04 ± 0.01	0.09 ± 0.00
MBC (μg g^{-1})	0–10	248.83 ± 1.90	226.21 ± 15.44	136.84 ± 7.32	286.22 ± 14.23	281.57 ± 19.4	149.14 ± 29.58	154.52 ± 0.57	167.24 ± 15	131.62 ± 6.99
	10–20	188.22 ± 12.4	160.74 ± 0.88	157.62 ± 7.09	106.83 ± 3.93	260.42 ± 29.22	129.16 ± 23.75	79.59 ± 19.29	110.39 ± 9.5	103.79 ± 4.71
MBN (μg g^{-1})	0–10	15.43 ± 0.36	11.16 ± 2.08	6.86 ± 1.66	17.50 ± 2.36	11.94 ± 2.86	10.03 ± 3.26	11.05 ± 2.70	7.97 ± 2.60	8.47 ± 3.10
	10–20	8.46 ± 0.01	10.40 ± 3.27	5.97 ± 1.19	14.33 ± 0.72	9.30 ± 4.18	5.25 ± 0.03	7.60 ± 3.04	7.53 ± 2.01	7.54 ± 2.15
MBC/SOC	0–10	2.38 ± 0.36	2.32 ± 0.70	2.28 ± 0.48	1.28 ± 0.00	2.50 ± 0.93	2.09 ± 0.39	2.71 ± 0.24	2.59 ± 0.23	4.27 ± 0.30
	10–20	4.05 ± 0.46	4.33 ± 0.63	5.26 ± 0.08	1.75 ± 0.11	6.07 ± 1.20	3.97 ± 0.94	4.04 ± 1.33	3.95 ± 2.04	9.60 ± 0.18
MBN/TN	0–10	0.67 ± 0.15	0.48 ± 0.08	0.61 ± 0.19	0.60 ± 0.05	1.23 ± 0.72	1.22 ± 0.53	0.49 ± 0.05	0.34 ± 0.11	0.58 ± 0.17
	10–20	0.36 ± 0.01	0.74 ± 0.24	0.60 ± 0.12	0.37 ± 0.04	0.94 ± 0.55	0.83 ± 0.56	0.36 ± 0.15	2.03 ± 0.94	0.82 ± 0.27
MBC/MBN	0–10	16.13 ± 0.50	20.72 ± 2.49	21.45 ± 6.27	16.54 ± 1.41	25.43 ± 7.72	15.55 ± 2.11	14.88 ± 3.70	24.16 ± 9.77	22.02 ± 6.28
	10–20	22.23 ± 1.52	17.18 ± 5.49	27.7 ± 6.70	7.48 ± 0.65	36.81 ± 19.67	24.53 ± 4.34	13.65 ± 7.99	16.13 ± 5.57	15.54 ± 3.18
C/N	0–10	4.75 ± 1.61	4.59 ± 1.14	5.52 ± 1.31	7.75 ± 0.11	13.51 ± 8.55	8.31 ± 1.20	2.67 ± 0.59	2.81 ± 0.02	2.75 ± 0.13
	10–20	2.01 ± 0.01	2.69 ± 0.37	3.04 ± 0.08	1.65 ± 0.44	4.13 ± 1.11	7.23 ± 6.12	0.96 ± 0.12	8.84 ± 3.60	14.59 ± 4.28

Table 3 Results of two-way ANOVA to analyse the effect of disturbance and invasion and their interaction on soil physical and biochemical parameters

Parameters	Source of variation	df	SS	MS	F-value	P-value
Moisture Content	Disturbance	2	17.81	8.91	0.712	0.50
	Species	2	125.44	62.72	5.01	0.02*
	Disturbance × Species	4	209.65	52.41	4.18	0.01*
pH	Disturbance	2	0.204	0.10	0.38	0.68
	Species	2	2.46	1.23	4.65	0.02*
	Disturbance × Species	4	1.45	0.36	1.37	0.28
BD	Disturbance	2	0.02	0.01	0.88	0.43
	Species	2	0.67	0.34	20.06	< 0.001***
	Disturbance × Species	4	0.11	0.03	1.6	0.22
SOC	Disturbance	2	0.16	0.08	0.62	0.54
	Species	2	0.64	0.32	2.50	0.11
	Disturbance × Species	4	3.06	0.76	5.90	0.004**
TN	Disturbance	2	0.01	0.005	0.89	0.42
	Species	2	0.02	0.01	1.90	0.18
	Disturbance × Species	4	0.07	0.02	3.37	0.03*
MBC	Disturbance	2	26,916	13,458	1.74	0.20
	Species	2	4922	2461	0.32	0.731
	Disturbance × Species	4	41,624	10,406	1.35	0.29
MBN	Disturbance	2	42.65	21.32	7.94	0.004**
	Species	2	310.97	155.49	57.88	< 0.001***
	Disturbance × Species	4	232.06	58.01	21.59	< 0.001***
MBC/SOC	Disturbance	2	5.95	2.97	0.65	0.53
	Species	2	4.76	2.38	0.52	0.60
	Disturbance × Species	4	21.92	5.48	1.20	0.35
MBN/TN	Disturbance	2	0.38	0.19	1.57	0.23
	Species	2	0.01	0.01	0.07	0.92
	Disturbance × Species	4	0.84	0.21	1.75	0.19
MBC/MBN	Disturbance	2	1182	590.9	1.6	0.23
	Species	2	1086	543.2	1.47	0.26
	Disturbance × Species	4	2793	698.4	1.89	0.16
C/N ratio	Disturbance	2	5.63	2.81	0.43	0.66
	Species	2	0.12	0.06	0.01	0.99
	Disturbance × Species	4	55.21	13.80	2.09	0.13

df degrees of freedom, *SS* Sum of Squares, *MS* Mean sum of Squares. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

of the soil. MBN did not change along the disturbance gradient in surface soil layers, however, in the lower soil layer MBN was found significantly high in the MD site under *L. camara*-occupied soil (Fig. 4 k, l) .

The relative contribution of disturbance and invasion on soil physical and biochemical properties

The principal component analysis (PCA) showed variation among soil physical and biochemical properties under the native and invasive plant species across the different gradients of disturbance (Fig. 6). The PCA plot identified two axes (PC1 and PC2) of variation that explained about 36% and 23% variation respectively (Table 4). The PCA indicated that the differences between the soil properties of both native and invasive species across the three sites occurred, although to a different extent: *A. vasica* showed greater differences among the three sites than *L. camara* (Fig. 6). Further, variance partitioning test was conducted to quantify the relative contribution of disturbance and species invasion on soil properties using the Venn diagram (Fig. 7). The explanatory variables used for the analysis were grouped into four classes: Disturbance, Species type (invasive vs. native species), Soil depth and Vegetation parameters (density and basal area of tree and shrub layer). Overall, 87% variation in soil properties was explained by the explanatory variables. Among the various attributes,

Table 4 Loadings (in %) of the soil physical and biochemical variables in the Principal Component Analysis (Fig. 6). Shown are the first four principal components for which the eigenvalues are > 1

PCA loadings	Dim.1	Dim.2	Dim.3	Dim.4
Moisture	21.18	0.77	0.71	1.02
pH	7.19	7.97	1.78	8.77
BD	17.99	0.004	0.19	3.70
SOC	13.52	12.33	0.94	4.6
TN	11.47	2.71	15.6	0.32
MBC	12.68	1.33	18.91	1.17
MBN	9.68	4.27	5.96	19.03
MBC. SOC	1.13	17.35	10.25	23.71
MBN. TN	3.66	15.36	4.16	29.10
MBC.MBN	1.40	10.71	28.71	8.32
C. N ratio	0.04	27.14	12.69	0.15
Eigenvalue	3.95	2.49	1.791	1.140
Variance percent	35.97	22.66	16.28	10.36
Cumulative variance percent	35.97	58.63	74.9	85.28

maximum variation was explained by disturbance (37.8%) followed by species type (33.3%), vegetation (16.4%), and soil depth (2.3%). The value of fractions with shared variance was not very high. Thus, the Venn diagram reflected that variance partitioning among the explanatory variables explained significant variation in soil properties.

Discussion

Impact of *lantana* invasion on species density, diversity and basal area across disturbance gradients

Our results showed that varying intensity of disturbance and invasiveness significantly impact species density, basal area and diversity. Present findings highlighted that in MD, where invasive LC dominates, the density of native shrubs (AV) was reduced. As already known, any events of disturbance such as grazing, lopping, logging and various roadside disturbances such as trampling, walking as well as foraging/grazing by wild animals are known to shape species composition and diversity (Bennett et al. 2012; Mandal and Joshi 2015). In highly disturbed sites, invasive *L. camara* remains dispersed along the edges of the roads showing maximum density and basal area in HD sites. This also impacted the distribution of canopy layer species that showed lower tree density in HD sites (Table S1). This suggests that roadside disturbance holds the key to the proliferation of invasive species (Gelbard and Belnap 2003; Khatri et al. 2022). Lower tree density in HD sites might also have led to the creation of canopy gaps which play an important role in the invasion of alien species by providing a new niche and adequate amount of light availability (Parendes and Jones 2000; Sharma and Raghubanshi 2011). Such invasive alien species are known to be highly dependent on increased light intensity and are capable of invading open canopy areas compared to densely vegetated areas (HOBBS and ATKINS 1988; Glasgow and Matlack 2007). Our results also lie in line with other studies conducted in invasive-prone regions (for instance *Prosopis juliflora* invaded sites) (Lins et al. 2018; Singh et al. 2022). Tree species richness and diversity were found to be maximum in the least disturbed sites, whereas shrub species and diversity were found maximum in highly disturbed sites. This could be again possible due to the recruitment of new species in highly disturbed sites due to scattered canopy (Singh 2021). Several research have concluded that increased levels of disturbances provide higher opportunities for species turnover, establishment and aggregation thus leading to increased species richness and diversity (Inderjit 2005; Malik et al. 2014).

However, our results contradict few studies that suggest a positive correlation between the vegetation density of native and invasive species (Hill et al. 2005). We found the opposite trend because the effect of disturbance acted as a catalyst that provides the key to the growth of invasive species in highly disturbed sites ultimately lowering the growth of native species (Lembrechts et al. 2016). Our results also do not support the general hypothesis that IAS can act as nurse species which facilitates the regeneration of native species (Selwyn and Ganesan 2009; Naudiyal et al. 2017). We also found that the importance value index (IVI) of invasive *L. camara* was maximum in HD, whereas IVI of native species was high in LD site, implying a negative effect of disturbance on the regeneration of native species, which could be due to high disturbance intensity resulting in loss of native shade-tolerant species (Mani and Parthasarathy 2006; Sunil et al. 2011).

Influence of native (*Adhatoda vasica*) and invasive (*Lantana camara*) shrub species on soil properties in LD, MD and HD sites

Our results indicated that the relative contribution of invasive *L. camara* and native *A. vasica* was high in MD and LD sites respectively. An increasing level of disturbance enhances the invasion of exotic shrub species i.e., *L. camara* and consequently increases the soil nutrient contents (Fig. 4 and Table 2). However, intense human interference in HD sites reduces soil fertility and causes tree mortality. In the MD site, soil moisture, SOC, and MBC were significantly higher as compared to the HD site. It could be due to the high density of *L. camara* species in the MD site which might help to retain the soil moisture content through curbing the direct hit of solar radiation to the soil surface.

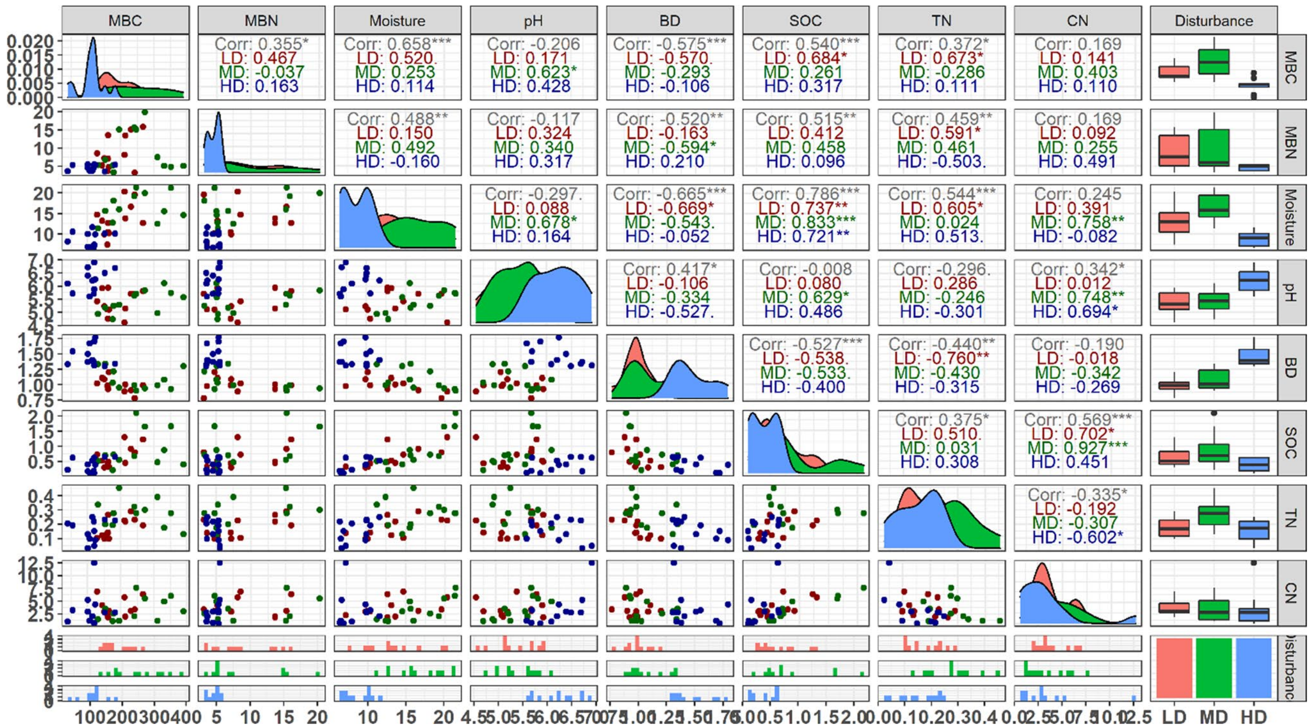

Fig. 5 Plot demonstrated the association between the soil physical and biochemical properties. Lower triangle showed scatter plot and, the upper triangle indicated the association among the soil properties at a significant level (as star). p value 0.001 (***), 0.01 (**) and 0.05 (*). *SOC* = soil organic carbon, *TN* = soil total nitrogen, *BD* = bulk density, *CN* = C/N ratio, *MBC* = soil microbial biomass carbon, *MBN* = soil microbial biomass nitrogen

In addition, correlation analysis showed a strong positive association between SOC and moisture content (r = 0.78, $p = 0.001$) and between MBC and moisture content (r = 0.65, $p = 0.001$) (Fig. 5), found similar to previous studies (Kumar et al. 2023; Gupta et al. 2024). The values of soil properties agree with the previous study performed by (Tomar and Baishya 2020) in the semi-arid region of the Delhi ridge.

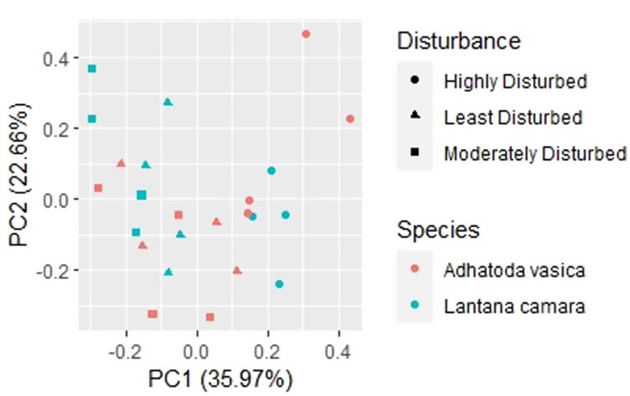

Fig. 6 Variation of soil properties among the disturbed sites under the two plant species (native: *A. vasica*) and invasive: *L. camara*) as analyzed by Principal Component Analysis (PCA). The three symbols represent different sites whereas the colors (red and blue) represent the plant species

MBC changed significantly ($p < 0.05$) with the soil depth in *L. camara* and *A. vasica*-occupied regions, while in bare soil no significant difference was observed with the soil depths. Higher MBC in the upper layer of *L. camara* and AV-occupied sites might be attributed to higher bulk density and low soil moisture content. Higher bulk density reduces pore spaces between the soil particles which consequently leads to decrease in microbial activity (Kumar et al. 2021; Kumar and Garkoti 2022). Another reason for increased MBC could be due to increased tree density and diversity in LD and MD sites. This leads to an increased amount of litter accumulation due to increased vegetation cover in low and moderately disturbed sites (Arunachalam et al. 1996). Present findings were consistent with other studies in different forest ecosystems such as Himalayan sub-tropical and temperate forests (Arunachalam et al. 1996; Chandra et al. 2023).

Synergistic effect of disturbance and invasion on soil properties

Overall, we found the combined effect of disturbance as well as invasion that significantly affects the growth and distribution of native species. This was also reflected through the PCA plot that explained around 58% of variation

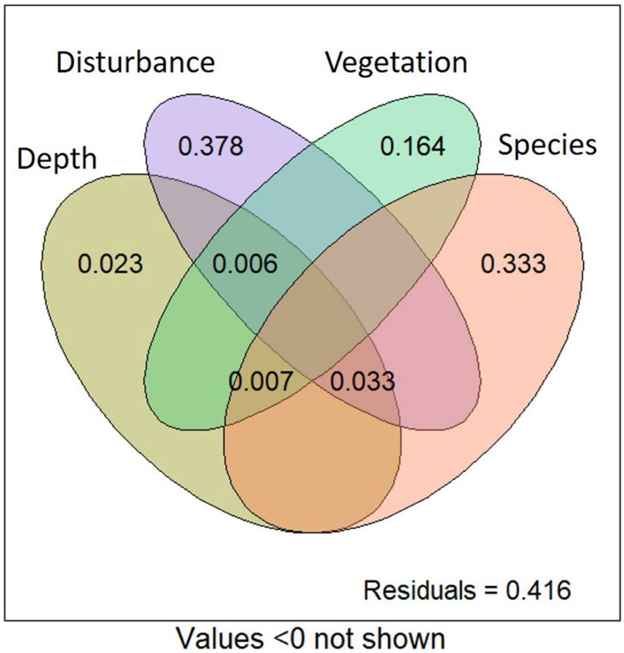

Fig. 7 Venn diagram showing the partitioning of variation according to four groups of independent variables, Soil Depth, Disturbance, Vegetation, and Species type. The rectangle corresponds to the total variation in the dependent (soil properties) data. Each area of overlap of the four ellipses is representative of the intersection of the four groups in terms of their explained variation. The area of the rectangle (total variation) that the four ellipses do not cover represents the unexplained variation (residuals)

caused due to disturbance gradients and species invasion. PCA plot also indicated that the differences between the soil properties across the sites were higher for *A. vasica* than *L. camara* (Fig. 6). This suggests that such IAS are also known to modify the environmental conditions that create variation in soil properties which ultimately affects the abundance and distribution of native species (Wallace et al. 2017). Variance partitioning analysis suggested the soil properties to be maximally affected by disturbance (~37%) followed by species type (~33%) (Fig. 7). In general, species (native or invasive) shift towards facilitation as stress increases (He et al. 2013). This suggests species adapt to changing environmental conditions which leads to modification in community assembly processes (Willis et al. 2010). Moreover, unexplained variation (residuals = 0.416) in soil properties across sites further suggests the importance of considering additional factors such as competition among species and biotic stress to understand the mechanisms behind variation in soil properties of native and invasive species-dominated sites along disturbance gradient (Chytrý et al. 2008).

Conclusion

In the present study, the coupling effect of disturbance and plant invasion was observed on vegetation attributes and associated soil physical and biochemical properties. Tree density and basal area were found higher in the LD, whereas shrub density was found higher in the HD, moreover, shrub total basal area was found maximum in LD followed by the HD site. In HD sites, low ground cover and open canopy provide prerequisites for the invasion of *L. camara* that consequentially leads to increased shrub density. Shrub diversity and species richness were also observed maximum in HD sites while tree diversity and species richness were found to be maximum in LD sites. The higher density of LC in HD sites largely reduces the below-ground soil nutrients, by incorporating the soil nutrients efficiently. However, with increasing disturbance and invasion, we found lower values for soil nutrients and microbial biomass. PCA plot revealed that both disturbance and plant invasion contribute to around 58% variation in soil properties. The study lies in agreement with the proposed hypothesis that high disturbance alters the vegetation attributes and associated soil properties, which ultimately promotes the invasion of *L. camara.* The variance partitioning suggested that data variability was primarily explained by disturbance followed by vegetation attributes. Though the present work is constrained by a limited sampling area, which may restrict the comprehensive analysis of the effect of invasion across disturbance gradient, we recommend a more robust scientific approach to replicate the research using a larger sampling region to enable a thorough investigation of the coupled effect of invasion and disturbance on vegetation and soil health.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11258-024-01441-6.

Author contributions Research work was designed by Priya Hansda (PH) and Satish Chandra Garkoti (SCG) and fieldwork was performed by PH, Shailendra Kumar (SK) and Shipra Singh (SS). The experimental work and data interpretation was performed by PH and SK. PH has written the manuscript and it has been edited by SCG, SS and SK.

Funding The financial support was provided by the University Grants Commission (UGC) and DST-PURSE, Government of India.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors have not disclosed any competing interests.

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