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How *Lantana* invades dry deciduous forest: a case study from Vindhyan highlands, India

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Abstract: Invasion by exotic species is among the most important global-scale problems experienced by natural ecosystems. Studies document that floristic changes that emerge after habitat fragmentation may be due to invasion by exotic weeds. When either habitat modification or the introduction of foreign species results in changes in the community, then native species populations could undergo local decline or extinction. The present study provides a qualitative and quantitative overview of the effects of habitat fragmentation on the invasive success of *Lantana camara* as well as the subsequent effects of this invader on ecosystem structure and function in the Vindhyan dry deciduous forest of India.

Resumen: La invasión de especies exóticas es uno de los problemas mundiales más importantes que experimentan los ecosistemas naturales. Hay estudios que documentan que los cambios florísticos posteriores a la fragmentación del hábitat pueden deberse a la invasión de malezas exóticas. Si la modificación del hábitat o la introducción de las especies foráneas producen cambios en la comunidad, entonces las poblaciones de especies nativas podrían sufrir declinaciones o extinciones locales. El presente estudio ofrece una visión general cualitativa y cuantitativa de los efectos de la fragmentación del hábitat sobre el éxito invasor de *Lantana camara*, así como los efectos subsecuentes de esta invasora sobre la estructura y la función del ecosistema en el bosque seco caducifolio de Vindhyan, India.

Resumo: A invasão por espécies exóticas está entre os problemas mais importantes experimentados pelos ecossistemas naturais à escala global. Os estudos documentam que as mudanças florísticas que emergem depois da fragmentação do habitat podem ser provocadas pela invasão por infestantes exóticas. Quer quando se verificam mudanças no habitat, ou quando, pela introdução de espécies exóticas, se verificam mudanças na comunidade, então as populações de espécies nativas podem entrar em declínio local ou extinção. O estudo presente proporciona uma revisão qualitativa e quantitativa dos efeitos da fragmentação do habitat pela invasão de sucesso da *Lantana camara* bem como dos efeitos subsequentes desta invasora na estrutura e funções do ecossistema na floresta decídua seca de Vindhyan da Índia.

Key words: Dry deciduous forest, habitat fragmentation, plant invasions, *Lantana camara*, Vindhyans.

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Introduction

Modern human-dominated landscapes are typically characterized by intensive land-use and high levels of habitat destruction, often resulting in sharply contrasted habitat mosaics. Fragmentation of remaining habitat is a major threat to biodiversity (Tscharntke *et al.* 2002) and ecosystem functioning (Didham *et al.* 1996; Kareiva & Wennergren 1995). Decreasing size and increasing isolation of habitat patches lead to decline in species richness and abundance as well as changes in community structure (Dewenter *et al.* 2002). This process of habitat fragmentation and destruction may greatly change the landscape structure and local ecosystem functioning (Kareiva & Wennergren 1995).

After habitat fragmentation plant communities become more susceptible to invasion by non-native plant species (Bennett 1999). Studies by Laurance *et al.* (1998) documented that floristic changes emerge after habitat fragmentation, which may be due to invasion by exotic weeds. Janzen (1986) also reported that fragments of tropical dry forest in Costa Rica are prone to invasion by weedy generalist plant species. When changes in community occur either through habitat modification or through the introduction of foreign species, local decline, and even extinction of native species may occur (Pimm 1986). The effect of fragmentation on species loss is now becoming well known (Cody 1993). However, few studies have looked at the effects of fragmentation on the success of invaders as well as the subsequent effects of the invader on the native species resident in fragments.

We provide a qualitative and quantitative overview of the effect of habitat fragmentation on invasive success of *Lantana camara* L. (lantana) in the Vindhyan highlands. The objectives of our study were to elucidate the following: (a) The dynamic interactions between forest fragmentation and invasive species; (b) The effect of canopy opening on invasive cover; (c) The effect of invasion on herb species composition and soil properties; (d) The effect of invasion intensity on the decline of tree species populations; and (e) The effect of plant invasion on soil process, especially N-mineralization.

Study area and methods

The study area is in the Vindhyan highlands, and lies between 83° 00´ and 83° 15´ E, and 24° 00´ and 24° 30´ N, covering predominantly the Renukoot forest division of Uttar Pradesh, India (Fig. 1). The elevation above mean sea level ranges between 313 and 483 m (Sagar & Singh 2004). The climate of the area is tropical monsoonal with distinct rainy, winter, and summer seasons. Soils are residual ultisols, sandy loam in texture, reddish to dark grey in colour, and extremely poor in nutrients (Sagar & Singh 2004). The potential natural vegetation of the study area is dry deciduous forest, locally dominated by *Adina cordifolia, Lagerstroemia parviflora, Butea monosperma, Soymida febrifuga, Hardwickia binata*, and *Acacia catechu,* with or without *Shorea robusta* in different combinations (Jha & Singh 1990; Sagar & Singh 2004). The forest in the area is under heavy biotic pressure. Past studies in the region have also shown that the Vindhyan dry deciduous forest has been fragmented extensively and these fragments are being invaded by exotic plants, particularly lantana (Goparaju *et al.* 2005; Goparaju & Jha 2010; Raghubanshi & Tripathi 2009; Tripathi 2003). The present study was carried out between 2001 and 2004. A reconnaissance survey was undertaken for the entire region and three sites, *viz.* Rajkhar, Baheradol, and Hathinala, were selected at random to represent the entire range of conditions in terms of canopy cover and vegetation. At each site three fragments were selected, each representing a different fragment size class, namely, small (<1 ha), medium (1-10 ha), and large (>10 ha). Fragments were selected based on remotely sensed imagery and a reconnaissance of the area.

In each fragment ten 10 x 10 m quadrats were established in a belt transect from the edge to the interior of the fragment. Vegetation was sampled in these quadrats following standard methodologies. Forest fragments considered for the present study are prominently forest areas broken up by highways and forest roads. Vegetation was sampled during the year 2002 and 2003 in the month of October (for detailed methods see Sharma & Raghubanshi 2007).

Soil moisture in the top 10 cm of soil was measured in the field using the Theta Probe (Delta-T Devices Ltd., England) as the growing season average of drained soil (July to October, integrated). Light intensity below the canopy of selected stands was measured using a LCA-2 battery operated portable infrared carbon dioxide analyser having PAR sensors (filtered selenium photocell) (ADC Scinokem International, U.K.); 70-100 % sunlight (measured as PAR at 11.00 am on a

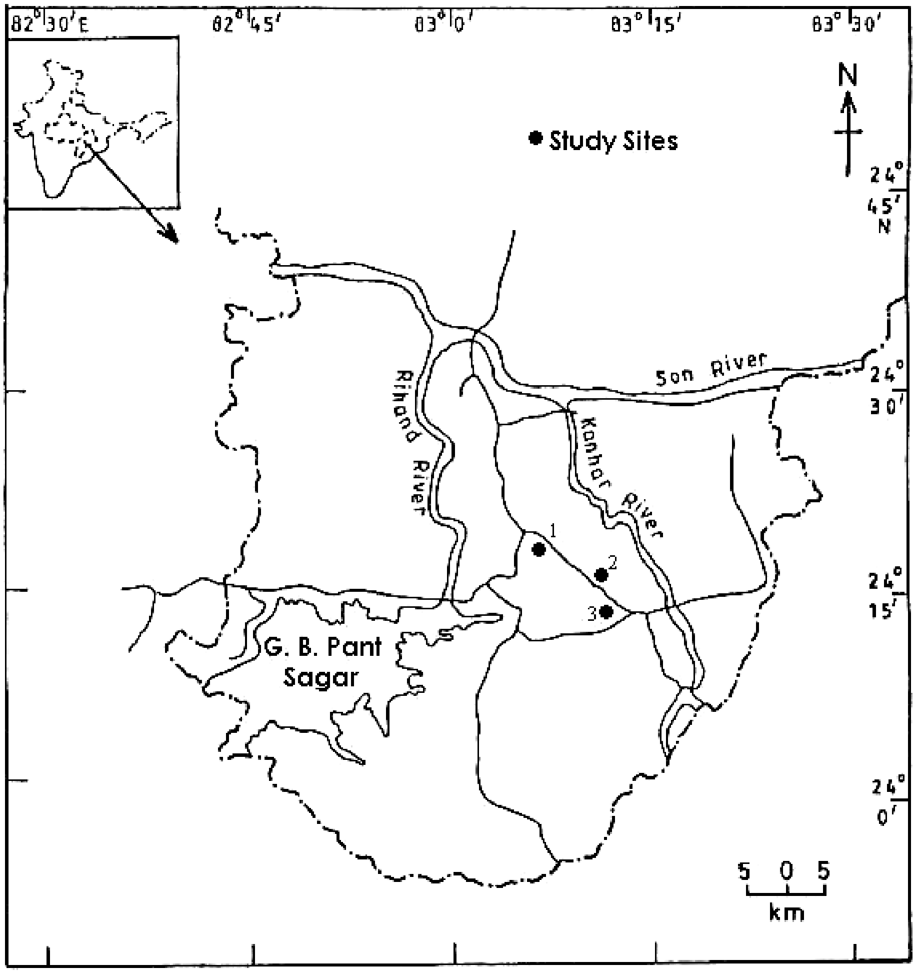

Fig. 1. Location of the study sites within the Vindhyan highlands, India: 1. Hathinala, 2. Bhaheradol, 3. Rajkhar.

cloud-free day) corresponded to photon flux density of 1,600-1,720 μmol m^{-2} s^{-1}. These shade levels are henceforth referred to as low (70-100 % sunlight/ ~ 30 % canopy cover), medium (30-60 % sunlight/ ~ 35-55 % canopy cover), and high (10-20 % sunlight/ ~ 60-70 % canopy cover) shade. Percentage light attenuation below lantana was calculated using the formula:

$$\%\ \text{Light attenuation} = \frac{\text{Light above lantana} - \text{Light beneath lantana}}{\text{Light above lantana}} \times 100$$

The attenuation of light beneath the lantana increased with increasing lantana cover, i.e., 40, 53 and 87 % attenuation for low, medium and high lantana cover respectively.

Results and discussion

Factors influencing the invasive success of Lantana camara

Disturbance

Dry tropical forests are one of the most threatened and least protected ecosystems of the globe (Wright 2005) and are highly disturbed. These forests supply approximately 90 % of the fuel wood and fodder needs of local populations, thus fuel wood collection may be a major contributor to forest degradation.

Frequent small-scale disturbances such as sporadic tree felling and lopping of trees can create localized patches or canopy gaps. Since such lopped wood loads can be easily removed from forest edges by local inhabitants, this leads to an increased number of canopy gaps at the edges. Previous studies suggest that disturbance may include structural changes in the community (e.g., amount of biomass removed or destroyed from disturbed patches), or changes in soil characteristics, or both (Armesto & Pickett 1985; Gentle & Duggin 1997a, 1998). In addition to such disturbances the habitat is being fragmented, and the Vindhyan highlands are now a mosaic of disturbed open-canopy patches and relatively undisturbed closed-canopy patches at several spatial scales (Jha & Singh 1990). Microclimatic changes near edges, for example, greater solar flux (Zuidema *et al.* 1996), create favourable conditions for edge species (Laurance 1991). Soil moisture regime is also altered along edges. These changed microclimatic conditions in fragmented forests favour establishment of opportunist and exotic species (Chen *et al.* 1992; Kapos 1989; Laurance 1991; Malcom 1994).

The presence of disturbance in the form of canopy openings increases resource availability and also modifies the microclimate, which is consistent with the disturbance patch invasion model (Gentle & Duggin 1997a). The model states that the removal of competitive biomass and disruption of interspecific competitive interactions creates patches of increased resources. Many of the exotic weeds benefit from edge environments and exert substantial pressure, including competition, on the range of native species (Fischer *et al.* 2006; Harper 2005; Ries *et al.* 2004). The success of invaders depends on the disturbance (Rejmanek 1989) and on the community involved (Forcella & Harvey 1983; Hobbs 1989; Orians 1986).

In the Vindhyan highlands, canopy openings, resulting from local disturbances, create patches of greater light availability. These canopy openings act as windows for invasive species (Johnstone 1986), particularly lantana in our case, because they provide a suitable combination of light regime and moisture level that is lacking in both the open as well as closed patches of the forests (Fig. 2).

Tree canopy cover varied from 23 % to 65 % and lantana cover varied from 52 % to 10 % from edge to interior of forest fragments (Fig. 2; Sharma 2006; see also Raizada *et al.* 2008). The effect of distance from edge to interior was significant both for tree canopy cover and lantana cover, and the later was significantly negatively related to tree canopy cover. At large local spatial scales (values of all the studied fragments integrated), lantana cover decreased with increasing tree canopy cover, and in locations with tree canopy cover > 63 %, no lantana was reported (Sharma 2006).

Light and moisture

The forests studied are heterogenous in terms of disturbed open-canopy and relatively undisturbed closed-canopy patches at several spatial scales (Jha & Singh 1990). Heterogeneous canopy opening results in a marked heterogeneity in terms of irradiance and temperature. Light availability on the forest floor has been recognized as a key factor that influences intrinsic traits of inhabiting species (Augspurger 1984; Bazzaz 1979; Jones *et al.* 1994; Kitajima 1994; Walters & Reich 1996) including invasive lantana (Raizada *et al.* 2008; Sharma 2006). Canopy openings resulting from local disturbance create patches of greater light availability (Rejmanek 1989), which act as an increased resource (Davis *et al.* 2000). In the Vindhyan highlands, edges had 70 to 85 % more light compared to intact forest. Chandrashekaran & Swamy (2002) have also reported that higher light availability under relatively open canopies enhanced the growth of lantana.

Soil moisture that we recorded ranged between 7.5-30 %. We found lantana growing in soils with moisture level between 10-25 %. In areas where soil moisture was < 10 %, no lantana was found, and this corresponded to large open patches. Soil moisture values above this critical level (10 %) at which lantana was found occurred only when stands had a certain level of tree canopy cover (Sharma 2006). Possibly both these factors - light and soil moisture - might restrict the establishment and colonization of lantana in intact forest (Fig. 2) (Sharma 2006). Lantana appears to perform best at intermediate levels of shade and this increases the overall performance of lantana, particularly the growth rate (Duggin & Gentle 1998; Islam *et al.* 2001) (Figs. 3 & 4).

Consequences of lantana invasion

Vegetation

Maximum lantana cover was reported at medium fragment size class, indicating that a critical size of fragment is required for the existence of maximum lantana cover and that below the critical fragment size lantana cover starts decreasing (Sharma 2006). Subsequent to plant species invasion marked changes in community composition, diversity, and ecosystem functioning occur (D'Antonio & Vitousek 1992). In the present study diversity and species richness showed a decreasing trend with increasing lantana cover (Fig. 5). Species richness and diversity of all species significantly decreased with increasing lantana cover. A similar trend was observed for species

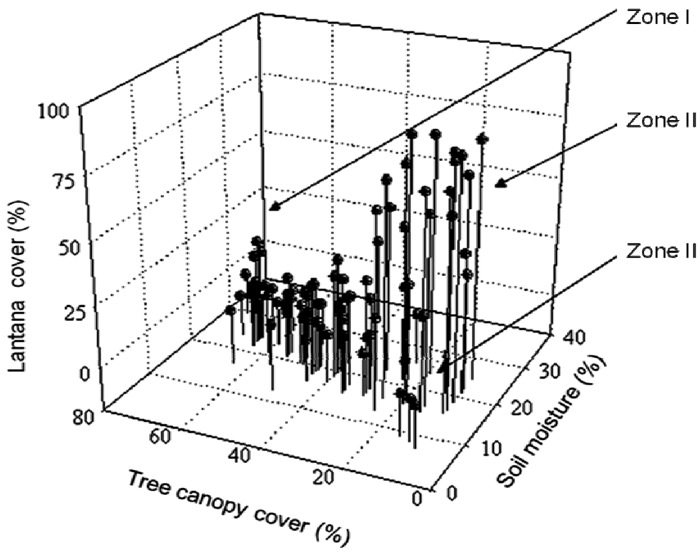

Fig. 2. Lantana exists at a critical moisture range, and its establishment is restricted both under dense shade and where the canopy is completely open. (Zone I: with high tree canopy cover, Zone II: critical moisture level where lantana exists luxuriantly and, Zone III: with large open patches).

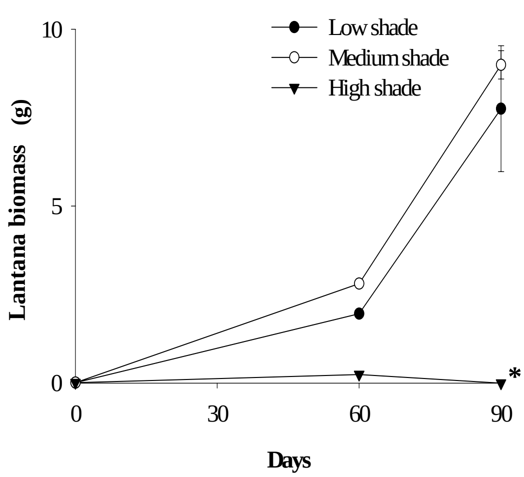

Fig. 3. Lantana biomass 60 and 90 days after being grown under different shade regimes (n=4) (Data from Sharma 2006).
*Seedlings died off due to extreme shade condition.

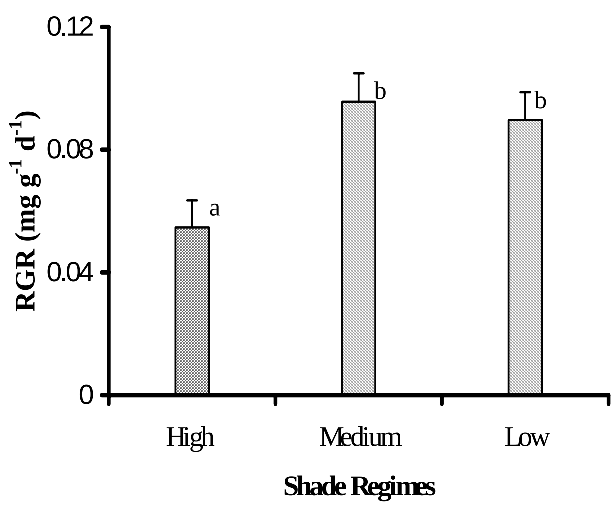

Fig. 4. Relative growth rate (RGR) of lantana grown under different shade regimes. Different letters indicate significant differences at $p < 0.05$ (Data from Sharma 2006).

richness and diversity of herbs (Fig. 5). Tree species richness showed a significant decrease with increasing lantana cover, although tree species diversity was not significantly affected (Fig. 5).

The results of our study conform to experimental models suggesting that with increasing invasive cover the diversity decreases (Stohlgren 2002). A study in tropical semi-evergreen

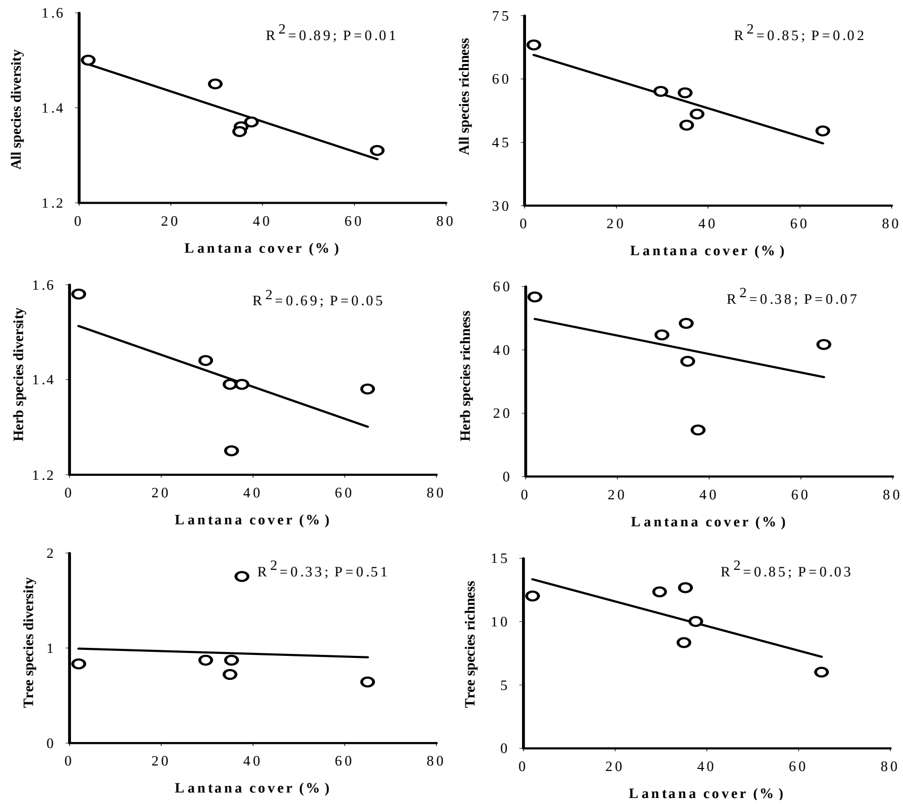

Fig. 5. Shannon-Wiener diversity (left) and Margalef species richness (right) as a function of lantana cover for all species (top), herbs (middle) and trees (bottom) (Data from Sharma 2006).

forests in Bangladesh also showed that invasion by lantana into forest gaps after human perturbation caused an abrupt decline in species richness (Islam *et al.* 2001).

Dense shade created by horizontal stratification of lantana reduces the intensity and duration of light, preventing the establishment of herbs and tree seedlings (Sharma & Raghubanshi 2006), resulting in marked changes in structural and floristic composition. The growth architecture of lantana also alters light microhabitat in its vicinity by addition of wood debris and above-ground litter, which is an important factor controlling herb species composition (Roberts 2004). Excessive amounts of leaf litter deposition make the site unfavorable for herbaceous species (Beatty & Sholes 1988; Roberts & Gilliam 1995) by damaging the existing plants (Halpern & Spies 1995), altering propagule availability (Stickeney 1990), and also by limiting recruitment due to lack of suitable habitats.

The accumulation of lantana litter and other broken debris could also lead to allelopathic suppression of regeneration of other tree species (Gentle & Duggin 1997b). Besides, allelopathy due to lantana could reduce early growth rates and selectively increase mortality of other plant species (Sharma *et al.* 2005a, 2005b), resulting in a reduction of species diversity and cover (Gentle & Duggin 1998; Loyn & French 1991).

Lantana is fire prone and can burn readily, altering the fire regime to favour its persistence (Hiremath & Sundaram 2005). The heat from burning lantana may also cause seed and seedling mortality in the area (Moore & Wein 1977). Thus, interaction of these factors with biotic pressure might inhibit both seed germination as well as seedling establishment, which may result in population decline. Thus invasive species cover may create demographic instability among tree species and reduce tree diversity, potentially changing the structure of the forest in the near future.

Species like *Anagallis arvensis, Barleria cristata, Dichanthium annulatum, Physalis minima, Setaria pumila* and *Sporobolus diander* that have limited distributions could be susceptible to further decline due to physical damage or altered habitat conditions with increasing lantana cover

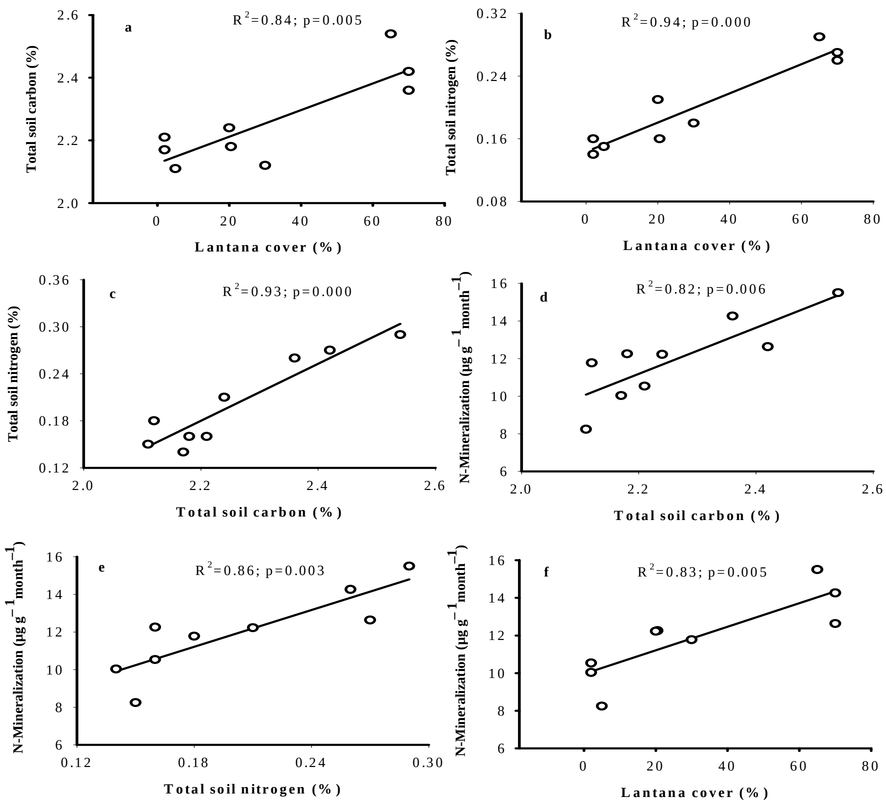

Fig. 6. Relationship among lantana cover, soil carbon, soil nitrogen and nitrogen mineralization (Data from Sharma 2006).

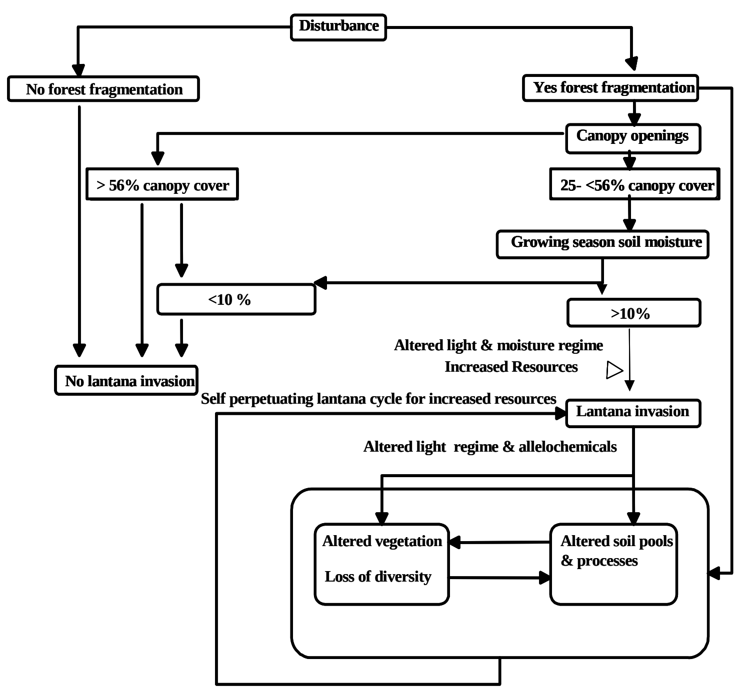

Fig. 7. A schematic diagram depicting the proposed effect of lantana invasion on ecosystem structure and function in the Vindhyan dry deciduous forest of India (adapted from Sharma 2006).

(Meier *et al*. 1995; Sharma 2006). Species like *Dichanthium annulatum, Evolvulus alsinoides, Leucas aspera, Malvastrum tricuspidatum, Rungia pectinata, Sida acuta, S. cordifolia, S. rhombifolia,* and *Tephrosia purpurea,* which decrease and ultimately become locally extinct with increasing levels of lantana cover may not recover quickly because of the altered physical environmental conditions (Sharma 2006). Species such as *Alysicarpus vaginalis, Andrographis echioides, Begonia picta, Ceropegia bulbosa, Cyanotis axillaris, Justicia simplex* and *Lindernia ciliata* that are unique to sites without lantana are highly sensitive to environmental perturbations, and are completely eliminated, locally, after lantana invasion (Sharma 2006).

Ecosystem process

Invasive species may contribute to modification of ecosystem process by providing a positive feedback that enhances their spread (D'Antonio & Vitousek 1992). Complex interactions between plant and soil, which cause soil properties to change in response to changes in plant species, may influence invasiveness (Ehrenfeld *et al.* 2001). So also, changes or shifts in plant community composition resulting from exotic invasions are likely to be associated with changes in soil properties as these are associated with natural succession processes (Ehrenfeld *et al.* 2001).

Invasion-mediated changes in the plant community will probably alter the quantity and quality of litter inputs and other soil properties (Bohlen 2006). These, in turn, could modify the system by altering rates of litter decomposition and accumulation and storage of organic matter as well as rates of nutrient release from the decomposing litter. Such changes could possibly create feedbacks for continued invasion (Kourtev *et al.* 2003; Wardle & Bardgett 2004).

Lantana traps wind-blown litter, and the denser the lantana cover, the greater its potential to trap litter. Trapped litter of other plant species and deposition of lantana litter leads to organic matter accumulation underneath its canopy, which increases with increasing lantana cover (Sharma 2006). Vitousek & Walker (1989) first pointed out that exotic species could alter soil processes. Changes in soil biogeochemistry following the shift in species composition could be another pathway of change (Vitousek 1990). This alternative mechanism would act indirectly via the effects of the introduced species on the soil biota and/or on the soil physical conditions, rather than directly through the traits of the invading species. Either mechanism could allow introduced species to create a feedback system (Wilson & Agnew 1992).

In the present study N-mineralization rate was significantly altered with increasing lantana cover (Fig. 6). Similar difference in soil processes and invasion are also reported in other instances (Asner & Beatty 1996; Kourtev *et al.* 1998; Vinton & Burke 1995). Data from different locations in the fragments also revealed that ammonification, nitrification and N-mineralization increased with increasing lantana cover (Fig. 6). In a study done in short grass steppe, higher N-mineralization rates were found in soil beneath the invasive plants *Kochia scoparia* and *Melinis minutiflora* (Asner & Beatty 1996; Vinton & Burke 1995). Kourtev *et al.* (1998) also reported increases in soil nitrification rates associated with the exotic species *Berberis thunbergii* and *Microstegium vimineum* in the deciduous forest of New Jersey.

Results of the present study suggest that lantana alters soil nitrogen dynamics, and that this effect increases with increasing lantana cover. Higher turnover rates of lantana litter, which reflect the rate of nutrient cycling, were reported for lantana in oak forests also (Rawat & Singh 1988). Rawat *et al.* (1994) reported that foliar nitrogen concentration of lantana was higher than that of other native species within the same habitat. Invasive species often maintain higher concentrations of leaf nitrogen (Ashton *et al.* 2005; Nagel & Griffin 2001; Vituousek *et al.* 1987) and consequently, are expected to decompose more rapidly and release more nitrogen to the soil than native species (Sharma & Raghubanshi 2009).

The changes in decomposition and nutrient cycling associated with lantana could have positive impacts on nutrient availability that could, in turn, further lead to greater decomposition in the invaded ecosystem (Hobbie & Vitousek 2000). This self-perpetuating nutrient availability due to faster N-mineralization could result in a higher availability of nutrients, subsequently leading to dense proliferation of lantana. It has been suggested that the combined influence of increased nitrogen and changes in light regimes associated with invasive species in grassland can facilitate further invasion and encroachment of such invasive species (Siemann & Rogers 2003). The same may be true in the case of lantana also.

Conclusions

There was a general increase in lantana cover with increasing fragmentation and also an inverse relationship between tree canopy cover and lantana cover. Maximum relative growth rate for lantana was found under low shade corresponding to the conditions at forest edges. Lantana invasion in fragmented forest may create demographic instability among tree species resulting in reduced tree diversity. Presence of lantana in dry deciduous forests alters the spatial pattern of herbaceous vegetation as lantana changes the microhabitat. Lantana alters light and nutrient availability, which may favour its self-perpetuation over the regeneration of other species. Thus, lantana invasion could change the structure of the forest in the near future. Increasing lantana cover also increases nutrient availability due to higher rates of soil N-mineralization. This leads to denser proliferation of lantana as other vegetation cannot compete with lantana's rate of growth (Fig. 7).

In conclusion, invasion of lantana in the Vindhyan dry deciduous forest is changing forest structure and resulting in a feedback system that accelerates lantana spread by promoting its competitive superiority over native species. This is leading to species diversity loss and the creation of a homogeneous, mono-specific lantana invaded understorey in the forest.

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