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Lantana camara invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation

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Abstract The effects of invasive species on community structure remain under-investigated due to the lack of long-term data. Our objectives were to examine the correlation between *Lantana camara* L. invasion and native species abundance, distribution, diversity, and population structure, across different forest types in a heterogeneous landscape. We examined changes in native vegetation and *L. camara* between 1997 and 2008. We used existing vegetation data from 134 plots spread across the 540 km^2 landscape from 1997 and re-censused these plots in 2008. We then examined the change in species richness, Shannon's diversity, evenness, and population structure of native species from 1997 to 2008. We also examined the relationship between *L. camara* density and species richness, diversity, evenness, and population structure. The presence and abundance of *L. camara* increased dramatically from 1997 to 2008. *L. camara* occurred in 81% of plots by 2008, compared with only 41% of plots in 1997. Similarly, the mean density of *L. camara* increased almost fourfold from 1997 to 2008. This was accompanied by a change in native community structure. Species richness, diversity and evenness declined significantly in some forest types, and at the landscape scale. There were also changes in the population structure of native tree species, with reductions in the density of tree saplings, possibly due to competition with *L. camara*. We demonstrate the pervasive threat posed by *L. camara* to native vegetation at the scale of individual forest types, and at the larger landscape scale, in our study area. These changes have long-term consequences for forest structure and composition.

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Introduction

Invasive species are significant drivers of ecosystem change. Invasive species alter or disrupt ecosystem processes such as nitrogen cycling (Ashton et al. 2005), hydrology (Strayer et al. 2006; Gordon 1998), native plant-pollinator mutalisms (Traveset and Richardson 2006), or below-ground mutalisms between native species and mycorrhizae (Stinson et al. 2006). Invasive

species are often better competitors than native species in the recipient habitat, resulting in community-level changes over the long-term (Strayer et al. 2006). In extreme cases, biological invasions lead to community disassembly due to competitive exclusion of native species by invasive species (Sanders et al. 2003), or rapid degradation of the entire ecosystem due to the predation of native species by invasive species (Fritts and Rodda 1998).

While the effects of invasive species on ecosystem processes are relatively well known, the impacts of invasive species on native communities are less well known, largely due to the paucity of long-term data (Strayer et al. 2006). To obtain detailed insights into the effects of invasive species on native communities, one needs to examine the response of a suite of community variables, e.g. species richness, diversity, abundance, evenness, population structure, and dominance (e.g. Hejda et al. 2009).

Invasive species can have negative impacts on the diversity and abundance of native species (Clavero et al. 2009; Gooden et al. 2009a; Hejda et al. 2009; Sanders et al. 2003). Studies show that biological invasions can lead to the homogenization of native communities (Hejda et al. 2009; Hillebrand et al. 2008; Olden 2006). Invasive species can also alter the population structure of native communities, leading to a change in the size class distributions of saplings or juveniles (Ens and French 2008; Sharma and Raghubanshi 2006; Litton et al. 2006) and changes in relative dominance within invaded communities (Fisher et al. 2009). Sakai et al. (2001) assert that invasive species often have an edge over native species in the competition for space due to recruitment advantages. Such advantages can result from prolific seed production and the lack of dispersal limitations for invasive species when compared to native species. Additionally, invasive species may gain competitive advantages in capturing space by the efficient use of resources in both high-nutrient (Huenneke et al. 1990) and low-nutrient (Funk and Vitousek 2007) conditions compared with native species.

Change in community variables as a result of species invasion may not be uniform across heterogeneous landscapes as compared to homogeneous landscapes (Melbourne et al. 2007; Strayer et al. 2006; Pauchard and Shea 2006). For example, forest type heterogeneity within landscapes is often determined by variations in topography and rainfall. Some forest types may be more invasible than others, while communities across different forest types may respond differentially to invasive species (Hejda et al. 2009). Therefore in heterogeneous landscapes, it is necessary to examine the response of community variables to invasive species at both the landscape scale and at the scale of individual forest types.

A large majority of studies that examine the effects of biological invasions on community structure or ecosystem processes use either historical records or space-for-time substitution (chronosequence) approaches to elucidate effects of invasive species on the structure of native communities. Studies that track the long-term response of native community diversity, abundance, evenness, population demography, and relative dominance to invasive species are rare, and valuable (Strayer et al. 2006). The principal advantage of long-term studies is that they do not require making assumptions about the past condition of a site, unlike studies that substitute space for time (Johnson and Miyanishi 2008; Landres et al. 1999). However, the frequency of monitoring confounding site conditions such as disturbance, determines the quality of data collected through long-term observations. Data from long-term studies that simultaneously track specific site conditions, such as disturbance along with other biological data are valuable (Magurran et al. 2010).

In this study, we take advantage of unique long-term data to examine the patterns of increase in density and spread of the invasive shrub, *Lantana camara* (Verbenaceae) hereinafter 'lantana', over 11 years. We examine the simultaneous change in native vegetation communities in different forest types of a landscape in the Western Ghats biodiversity hotspot, India. Our specific objective is to examine the long-term change in lantana distribution and abundance at both the landscape level and at the level of individual forest types. We predict that over the long term, native plant community variables such as species richness, diversity, evenness, and population structure will be negatively affected by an increasing lantana density, both at the landscape scale and at the scale of individual forest types. However, we are aware that correlation does not necessarily prove causation, and therefore we attempt to distinguish between cause and effect.

Methods

Study area

We conducted this study in the 540 km^2 Biligiri Rangaswamy Temple wildlife sanctuary (77°–77° 16′ E, and 11° 47′–12° 09′ N) hereinafter 'BRT'. The BRT terrain is hilly, with elevation ranging from 600 to 1,800 m above sea level. The sanctuary receives rainfall from both the southwest monsoon (June–September) and the northeast monsoon (October–December), with a pronounced dry period between January and March. There is considerable variation in rainfall with topography, with annual rainfall ranging from 898 to 1,750 mm, depending on location. The mean annual temperature in the study area is 25.3°C, and the temperature varies between a daily minimum of 11°C in winter and a daily maximum of 42°C in summer (Murali et al. 1998). Soils in BRT are well-drained, gravelly clays that have been classified as typic ustropepts (Anonymous 1996).

The BRT sanctuary is part of the Western Ghats biodiversity hotspot (Myers 2003; Mittermeier et al. 2004) and is located in the state of Karnataka, India. It was notified as a wildlife sanctuary in 1973 (Barve et al. 2005). The biodiversity of the area is rich, with at least 1,400 species of higher plants (Ramesh 1989; Kammathy et al. 1967). The main vegetation types in BRT are scrub-savanna, dry deciduous forest, moist deciduous forest, riparian semi-evergreen forest, evergreen forest, and the shola-grassland mosaic (Table 1). Seasonally dry forests comprising the scrub-savanna, and dry deciduous and moist deciduous forests, constitute approximately 90% of the study area (Ganesan and Setty 2004) and are now extensively invaded by lantana.

Lantana camara

Lantana camara L. is a multi-stemmed, woody straggling shrub native to Central and South America. Horticultural hybrid varieties of lantana (i.e. *Lantana camara* L. *sensu lato*) were introduced into India on multiple occasions (Cronk and Fuller 1995; Day et al. 2003; Sharma et al. 2005), with the earliest documented introduction dating back to 1,809 (Cronk and Fuller 1995). Within just over a century of its introduction, there were reports of lantana's invasiveness (Tireman 1916; Iyengar 1933; Anonymous 1942). Lantana is today a common invader of dry forest landscapes, slash-and-burn fallows, and pasture lands all over India (Sharma et al. 2005).

Information regarding the exact year of introduction of lantana into BRT is unavailable. Forest working plans mention the presence of lantana in BRT as early as 1934 (Ranganathan 1934), although interviews with the Soliga people, who have lived in BRT for centuries, suggest that the spread of lantana began during the 1970s (Sundaram 2011).

Change in lantana distribution in BRT (1997–2008)

In order to document a change in the density and abundance of lantana and native species, we took advantage of an earlier study in BRT, in which a grid-based, systematic sampling method was used to sample all vegetation, including lantana, between January and April 1997 (Murali and Setty 2001). We replicated this study in 2007–2008. The BRT area was overlaid by a 2 × 2 km grid, and a 5 × 80 m plot was laid at the centre of each grid cell. The GPS location of each plot in our study corresponded to the location of plots in the Murali and Setty (2001) study. Plots were located using a Garmin GPS 12XL fitted with an external antenna for added accuracy. Although we used the same geographical coordinates for our plots as Murali and Setty (2001), these plots may not have been in exactly the same locations due to errors associated with GPS triangulation. However, based on a comparison between the species encountered by Murali and Setty (2001) and the species we recorded, we believe we have closely approximated plots established by Murali and Setty (2001). Murali and Setty (2001) inventoried a total of 134 plots. However, by 2008, 12 plots had been transformed to non-forest (coffee plantation, human habitation, agriculture), leaving a total sample of 122 plots.

Within each 5 × 80 m plot, we recorded diameter at breast height (DBH) of all living woody vegetation ≥1 cm DBH. In the case of multi-stemmed plants, all stems ≥1 cm DBH were counted, and their DBH was measured. Individuals of all woody species were identified in the field whenever possible; samples of unidentified species were brought back to the field station and identified using floras and herbarium records. Vegetation in these 122 plots was sampled between August 2007 and January 2008.

Table 1 Classification of forest types in the Biligiri Rangaswamy temple wildlife sanctuary

Forest type	Attribute[a,b]		Characteristic species[c]
Scrub-savanna	Average rainfall (mm)	898	*Acacia chundra*
	Elevation range (m asl)	600–800	*Diospyros melanoxylon*
	Canopy height range (m)	4–6	*Chloroxylon swietenia*
Dry deciduous	Average rainfall (mm)	1,168	*Anogeissus latifolia*
	Elevation range (m asl)	800–1,100	*Terminalia crenulata*
	Canopy height range (m)	8–12	*Grewia tilaefolia*
Moist deciduous	Average rainfall (mm)	1,438	*Pterocarpus marsupium*
	Elevation range (m asl)	1,100–1,400	*Syzygium cuminii*
	Canopy height range (m)	15–20	*Terminalia bellerica*
Evergreen	Average rainfall (mm)	1,750	*Persea macrantha*
	Elevation range (m asl)	>1,400	*Litsea deccanensis*
	Canopy height range (m)	20–25	*Elaeocarpus tuberculatus*
Shola-grasssland	Average rainfall (mm)	1,750	*Memecylon umbellatum*
	Elevation range (m asl)	>1,400	*Cinnamomum zeylanicum*
	Canopy height range (m)	12–18	*Elaeocarpus serratus*

Plots were assigned to categories based on data from Ramesh (1989), Murali and Setty (2001); Ganesan and Setty (2004)

[a] Values are based on rainfall data from 1989 to 1999 from four recording stations situated in different areas of BRT; these stations correspond to the different forest types

[b] Range of canopy heights gathered from Ramesh (1989)

[c] Data from this study and Ramesh (1989)

For each plot, lantana presence and absence values for 1997 and 2008 were extracted. The densities of native species and lantana present during each sampling instance were calculated. For each plot, pairwise differences in the density of lantana and native species between 2008 and 1997 were then computed. The contribution to total basal area (total area occupied by stems within each plot) by lantana and by all other native species was also estimated.

For examining the change in lantana distribution (presence/absence, density, basal area) by forest type, the following forest types were distinguished: scrub-savanna, dry deciduous, moist deciduous and evergreen forest. Plots were assigned to forest type categories using information on species associations, canopy height, and elevation (Table 1). A Chi-squared test was used to examine differences in lantana density between 1997 and 2008.

Correlation between lantana invasion and native plant community structure

To examine the change in native plant communities over time, we computed (a) species richness (the total number of woody species in each plot), (b) Shannon's diversity index, H', and (c) Evenness, J. Values of community variables were calculated separately at the landscape level (which included all plots) and at the level of individual forest types (which included plots corresponding to each forest type), for 1997 and 2008. We also examined changes in relative dominance of all species between 1997 and 2008 in the different forest types by plotting rank-abundance curves. Rank abundance curves were plotted only at the level of individual forest type.

Shannon's diversity index, H' was calculated as $H' = -\sum_{i=1}^{S} \frac{n_i}{N} \ln \frac{n_i}{N}$ where n_i is the abundance of the ith species of S total species in the sample, and N is the density of all species in the sample (Stohlgren 2007). Evenness, J, was calculated using the formula $H'/\ln(S)$, where H' is Shannon's diversity index, and S is species richness (Magurran 1983). Since abundance is incorporated in the calculation of evenness, the index J is sensitive to dominance by any one or a few species. Values of J range from 0 to 1. Values closer to 0 indicate that the plot is dominated by a single species, while values of J closer to 1 indicate that all species are equally abundant.

In addition, we also examined changes in the population structure of trees, shrubs, and lianas between 1997 and 2008. Tree data were partitioned into three diameter (x) classes: $1 \leq x \leq 5$ cm DBH (small stems), $5 < x \leq 10$ cm DBH (medium stems), and $x > 10$ cm DBH (large stems). Small stems represent young regenerating trees, while medium and large stems represent adult trees. For the shrub and liana data, four diameter classes were chosen to reflect their stature: $1 \leq x \leq 2$ cm DBH, $2 < x \leq 4$ cm DBH, $4 < x \leq 8$ cm DBH, and $x > 8$ cm DBH. Size class data were examined for the entire landscape, and then separately at the level of each forest type.

Statistical analyses

The changes in means of various measures of community structure—species richness, S, Shannon's diversity, H', and evenness, J—that occurred simultaneously with lantana spread between 1997 and 2008 were analyzed at both the landscape-level and at the level of individual forest types, using a two-way repeated-measures ANOVA, with sampling year as the repeated measure and forest type as a factor. Post hoc Tukey's Honest Significant Difference (HSD) tests were used to determine treatment contrasts.

Since lantana density changed over time, species richness, Shannon's diversity, and evenness were also examined at the landscape scale and the forest-type scale using an ANCOVA. For the ANCOVA, the response of each of the three diversity estimates was examined in relation to forest type as a categorical variable, and lantana stem density as the independent covariate. Separate ANCOVAs were performed for the 1997 and 2008 data. Post hoc Tukey's HSD tests were used to examine treatment contrasts.

To determine changes in the population structure of woody native species the mean number of stems per size class per plot in 2008 was compared to corresponding values in 1997 using two-way repeated-measures ANOVA with sampling year as the repeated measure and forest type as a factor. Changes in population structure of trees and shrubs were analyzed statistically; liana data could not be subjected to the same analysis due to their small sample size. This analysis enabled us to determine whether changes in species density between years vary among different size classes. All statistical analyses were performed using R version 2.9.0 (R Development Core Team 2009).

Results

Long-term changes in lantana distribution across different spatial scales

Over 11 years, there was a tremendous increase in lantana abundance and density, both at the landscape scale, and at the level of individual forest types. At the landscape scale, lantana increased its spread from only 41% of the plots in 1997 (n = 134) to 81% of data plots by 2008 (n = 122) (Fig. 1). Results from the Chi-squared test indicated that lantana density increased significantly between years ($\chi^2 = 77.7$, $df = 5$, $P < 0.001$). The mean density of lantana increased more than threefold from 14.49 ± 2.21 stems/plot in 1997 to 53.76 ± 8.67 stems/plot by 2008. Moreover, by 2008, 32% of the invaded plots had a lantana density >50 stems/plot compared with 1997, when only 2.2% of the invaded plots had a lantana density >50 stems/plot (Fig. 1).

The pattern of change in lantana density at the landscape level was closely mirrored at the level of individual forest types, particularly the scrub-savanna, the dry deciduous and the moist deciduous forests. The mean density of lantana increased more than ten fold in the scrub-savanna and dry deciduous forests, and more than four fold in the moist deciduous forests (Table 2). Lantana density did not show an increase in the evergreen forest plots. However, a large proportion
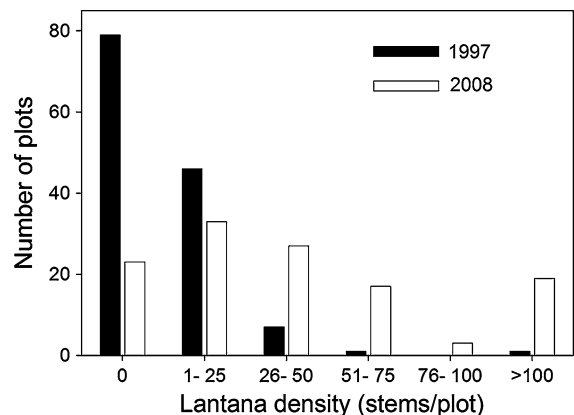
Fig. 1 Numbers of lantana stems per 400 m² plot encountered in 1997 and in 2008. In 1997, 134 plots were sampled; by 2008, 12 of these plots had been converted to other land uses, and so only 122 plots were sampled. A Chi-squared test indicated that differences between years were highly significant ($\chi^2 = 77.7$, $df = 5$, $P < 0.001$)

Table 2 Change in the density (stems/plot) of lantana and native species in the different forest types of BRT from 1997 to 2008. Sample sizes in each forest type are given within parentheses

Forest type	Lantana density (stems/plot)		t value	P	Native density (stems/plot)		t value	P
	1997 Mean ± SE	2008 Mean ± SE			1997 Mean ± SE	2008 Mean ± SE		
Scrub-savanna (n = 22)	3.22 (1.29)	44.71 (8.53)	4.53	0.001	178.27 (16.1)	89.0 (17.91)	3.95	0.001
Dry deciduous (n = 73)	4.79 (1.42)	48.99 (6.98)	6.26	0.001	96.7 (6.71)	72.41 (7.03)	2.75	0.007
Moist deciduous (n = 20)	12.65 (8.22)	60.25 (16.55)	2.42	0.016	95.7 (12.82)	107.85 (21.5)	0.58	0.566
Evergreen (n = 7)	7 (7)	0.29 (0.29)	–	–	149.43 (36.23)	112.57 (30.57)	0.89	0.407

Paired *t* tests were not conducted to compare change in mean density of lantana stems in the evergreen forest as lantana was present in only one plot in both 1997 and 2008

of evergreen forest plots (6 of 13; almost 50%) had been transformed into non-forest types by 2008, and only one plot in the evergreen forest had lantana present on both sampling occasions. The mean density of stems of native species showed significant declines from 1997 to 2008, of 50% in the scrub-savanna as well as 25% in the dry deciduous forest (Table 2). However, native stem density did not differ significantly between 1997 and 2008 in the moist deciduous and evergreen forest plots, which showed 13% increase and 25% decrease respectively (Table 2).

Although there was a tremendous increase in lantana density between 1997 and 2008, the proportion of total basal area accounted for by lantana in 2008 remained negligible when compared to the proportion of basal area contributed by all native species at the landscape level: 2% (Table 3). The contribution of lantana basal area to stand basal area at the level of individual forest types was negligible as well: between 0 and 4% across different forest types (Table 3).

Changes in dominance, species richness, diversity, and evenness across different spatial scales

The dominance structure of three of the four forest types changed quite noticeably from 1997 to 2008. Lantana became the most dominant species in terms of stem abundance (though not in terms of number of individuals) in the scrub-savanna and dry deciduous forests in 2008, with more stems of ≥1 cm DBH than the canopy tree, *Anogeissus latifolia*, which was dominant in 1997 (Fig. 2). Interestingly, lantana was already the dominant species (in terms of stem abundance) in the moist deciduous forest plots even in 1997, although it had augmented its dominance by 2008, with an almost four fold increase in stem abundance (Fig. 2).

There was a 22% decline in the mean native species richness per plot at the landscape scale from 1997 (15.83 ± 0.51) to 2008 (12.54 ± 0.52). From 1997 to 2008, there was also a decrease in total species

Table 3 Mean basal area (and standard error) of lantana and of native plant species in 1997 and 2008 at the landscape scale and at the level of individual forest types in BRT

	Basal area of lantana (m²/ha)		Basal area of all native species (m²/ha)	
	1997	2008	1997	2008
Entire landscape (n = 122)	0.08 (0.02)	0.52 (0.07)	28.59 (2.15)	26.20 (2.08)
Scrub-savanna (n = 22)	0.04 (0.01)	0.26 (0.02)	8.19 (0.39)	6.24 (0.43)
Dry deciduous (n = 73)	0.05 (0.01)	0.55 (0.07)	27.36 (0.91)	24.48 (1.55)
Moist deciduous (n = 20)	0.20 (0.05)	0.89 (0.11)	42.98 (2.80)	38.28 (2.33)
Evergreen (n = 7)	0.11 (0.03)	0.001 (0.0001)	60.54 (2.16)	69.90 (2.94)

Sample sizes in each forest type, and for the entire landscape, are given within parentheses

Fig. 2 Rank abundance profiles of all woody species by forest type in 1997 and 2008. *Labels* indicate the three most abundant species and lantana. Species and forest-type codes (in alphabetical order) are ANOLAT = *Anogeissus latifolia*, ATAMON = *Atalantia monophylla*, CHLSWI = *Chloroxylon swietenia*, CIPBAC = *Cipadessa baccifera*, DDF = dry deciduous forest, DIOOPP = *Dioscorea oppositifolia*, EGF = evergreen forest, ERYMON = *Erythroxylon monogynum*, HELISO = *Helicteres isora*, JUSSPP = *Justicia spp.*, LANCAM = *Lantana camara*, LITDEC = *Litsea deccanensis*, MAEIND = *Maesa indica*, MDF = moist deciduous forest, PSYSPP = *Psychotria spp.*, RANDUM = *Randia dumetorum*, SCR = scrub-savanna
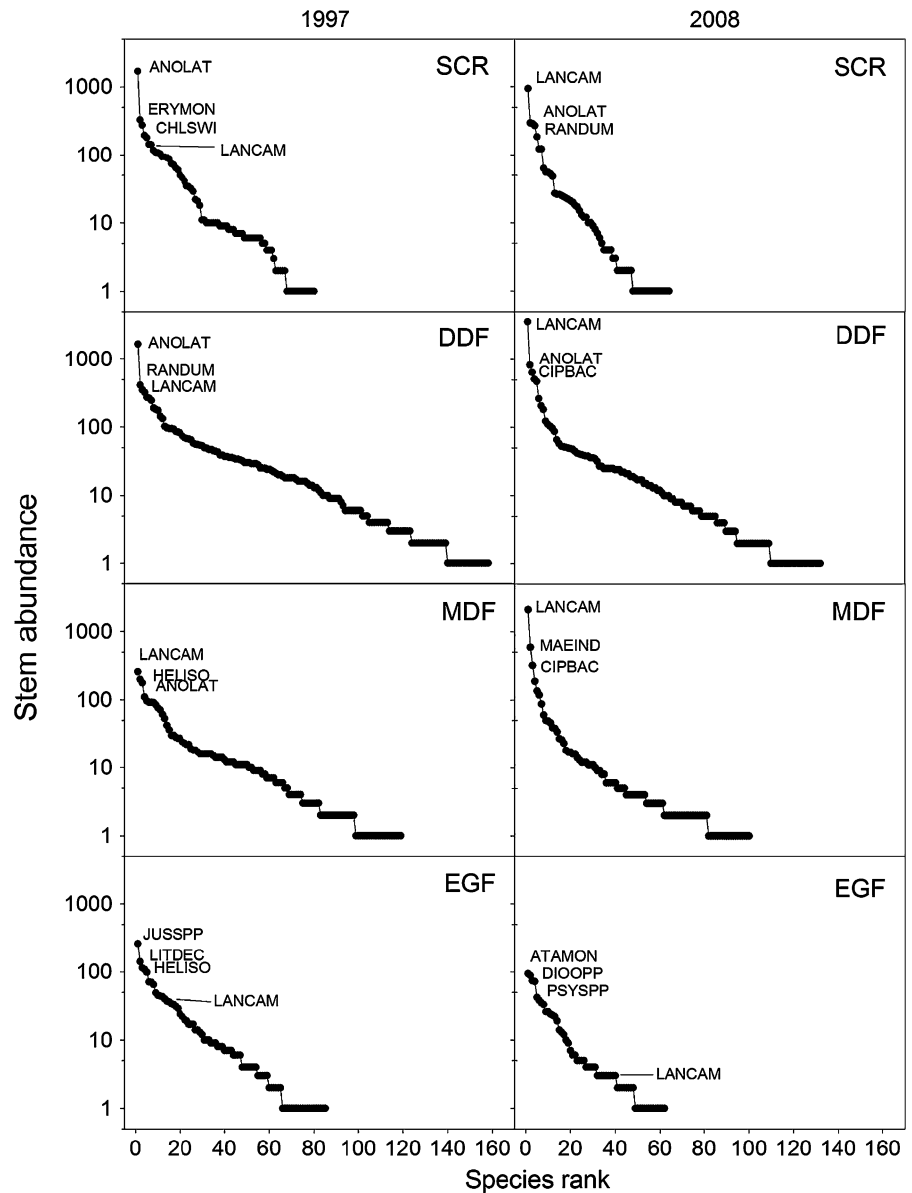
richness in all forest types, of 21% (from 80 to 63 spp.) in scrub-savanna, 16% (158–132 spp.) in dry deciduous forest, 16% (119–100 spp.) in moist deciduous forest, and 27% (85–62 spp.) in evergreen forest (Fig. 2). In the scrub-savanna, dry deciduous forests, and moist deciduous forests the decrease in mean species richness per plot between 1997 and 2008 was statistically significant (Table 4).

At the landscape scale, Shannon's diversity (H') of the woody species community was lower in 2008 (1.57 ± 0.05) when compared to 1997 (2.05 ± 0.04). Patterns at the landscape scale were mirrored by the pattern of change in H' the scrub-savanna, and in the dry- and moist-deciduous forests between 1997 and 2008. This decrease in diversity corresponded to a reduction in species richness in these forest types between 1997 and 2008. Plots in the evergreen forest did not change significantly in diversity from 1997 to 2008, mirroring patterns of similar species richness over the period 1997–2008 in this forest type (Table 4).

At the landscape level, values of evenness J were lower in 2008 (0.65 ± 0.02) when compared to 1997 (0.76 ± 0.01) and were correlated with an increase in lantana dominance. However, landscape-level patterns

Table 4 Species richness, Shannon's diversity H', and evenness J, in the different forest types of BRT in 1997 and 2008. Note that these are plot means

Forest type	Community variable	1997 Mean ($\pm$SE)	2008 Mean ($\pm$SE)	Source of variation		
				Time (P)[d]	Forest type (P)	Time*forest type (P)
Scrub-savanna	Species richness[a]	17.0 (0.92)	10.9 (1.32)	***	***	***
	Shannon H'[b]	1.9 (0.07)	1.6 (0.1)	***	***	***
	Evenness J[c]	0.71 (0.02)	0.71 (0.03)	ns	ns	ns
Dry deciduous	Species richness	14.6 (0.66)	11.7 (0.6)	***	***	***
	Shannon H'	2.0 (0.05)	1.5 (0.06)	***	***	***
	Evenness J	0.77 (0.01)	0.64 (0.02)	***	***	***
Moist deciduous	Species richness	17.6 (1.87)	14.1 (1.34)	***	***	***
	Shannon H'	2.1 (0.12)	1.5 (0.13)	***	***	***
	Evenness J	0.77 (0.03)	0.56 (0.01)	***	***	***
Evergreen	Species richness	17.7 (1.15)	18.3 (2.58)	ns	ns	ns
	Shannon H'	2.2 (0.12)	2.3 (0.16)	ns	ns	ns
	Evenness J	0.76 (0.05)	0.82 (0.02)	ns	ns	ns

The F values presented are from an ANOVA of each diversity measure as a response variable, time as the repeated measure, and forest type as a factor. The significance of sources of variation (Time, Forest type, Time x Forest type) within each forest type was determined using post hoc Turkey's tests

[a] Species richness varied significantly over time (ANOVA $F_{1, 117} = 24.99$, $P < 0.0001$), and across forest types (ANOVA $F_{3, 117} = 5.75$, $P = 0.001$), with a non-significant interaction between time and forest type (ANOVA $F_{3, 117} = 1.64$, $P = 0.18$)

[b] Shannon's diversity H' varied significantly over time (ANOVA $F_{1, 117} = 61.49$, $P < 0.0001$), and across forest types (ANOVA $F_{3, 117} = 4.62$, $P = 0.004$), with a significant interaction between time and forest type (ANOVA $F_{3, 117} = 3.32$, $P = 0.02$)

[c] Evenness J varied significantly over time (ANOVA $F_{1, 117} = 38.1$, $P < 0.0001$), and across forest types (ANOVA $F_{3, 117} = 2.84$, $P = 0.04$), with a significant interaction between time and forest type (ANOVA $F_{3, 117} = 7.29$, $P = 0.0001$)

[d] Values of P are indicated by ***($P < 0.0001$) and ns (non-significant)

were not reflected in the patterns observed at the level of individual forest types. Reduced evenness was observed only in the dry deciduous and the moist deciduous forests (Table 4). There was no evidence to support either increasing or decreasing evenness in the scrub-savanna and the evergreen forest plots (Table 4).

## Changes in population structure of native species at different spatial scales

The size-class distribution of native trees changed markedly over time at the landscape scale. There were significant reductions over time in the average density of stems in the smallest size classes (Fig. 3a). However, when data were analyzed separately by forest type, a significant reduction was evident only for small stems, and this was so in the scrub-savanna and dry deciduous forests (Figs. 3b, c). In the moist deciduous forests, on the other hand, the density of small stems remained statistically unchanged over time (Fig. 3d).

Tree data from the evergreen forest plots were not analyzed due to the small sample size.

The size-class distribution of native shrubs showed significant increases in the 1.0–2.0 cm DBH class at the landscape scale (Fig. 4a). The changes in the density of stems in all other size class were not significant at this scale. Patterns of the change in the size class distribution of shrubs seen at the landscape scale were mirrored by the dry- and moist deciduous forest plots, with significant increases in the density of stems in the smallest size class (Figs. 4c, d). The changes in the density of shrubs in the rest of the size classes in these forests were not significant. In the scrub-savanna, there was no statistically significant change in the population structure over time (Fig. 4b). Shrub data from the evergreen forest were not analyzed due to inadequate sample sizes. The mean density of native lianas was extremely low across all forest types (Fig. 5); hence we did not statistically analyse liana data.

Fig. 3 The mean number of native trees in each size class per plot, at the level of the landscape (**a**) and at the level of individual forest types, scrub-savanna (**b**), dry deciduous forest (**c**), and moist deciduous forest (**d**) in 1997 and 2008. Significant differences in tree density within a size class between 1997 and 2008 are indicated by *($P < 0.05$), **($P < 0.01$), or ***($P < 0.001$). Note difference in y-axis scale in the case of the scrub-savanna
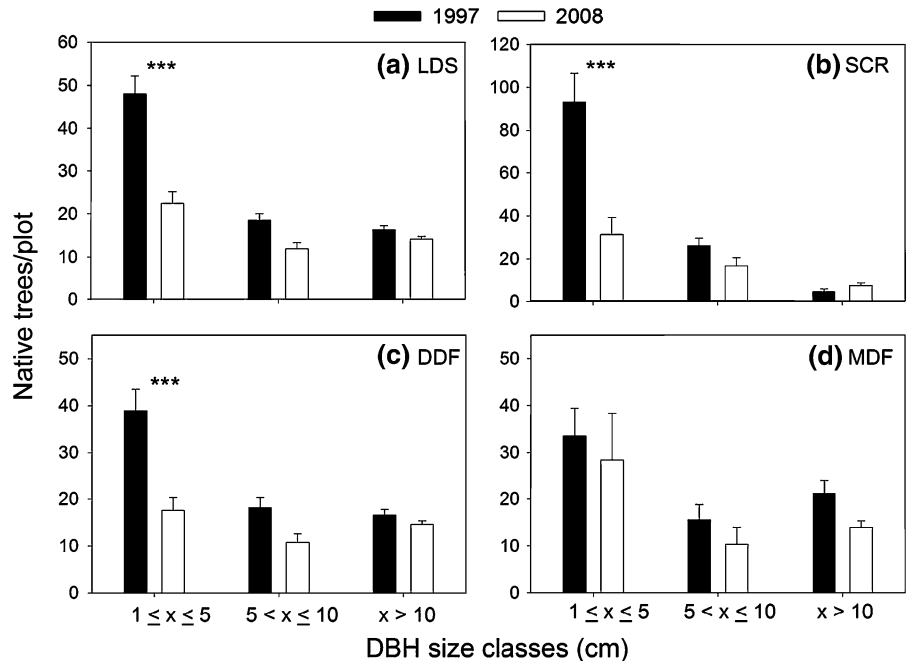
Fig. 4 The mean number of shrubs in each size class per plot, at the level of the landscape (**a**) and at the level of individual forest types, scrub-savanna (**b**), dry deciduous forest (**c**), and moist deciduous forest (**d**) in 1997 and 2008. Significant differences in shrub and liana density within a size class between 1997 and 2008 are indicated by *($P < 0.05$), **($P < 0.01$), or ***($P < 0.001$). Note differences in y-axis scale among panels
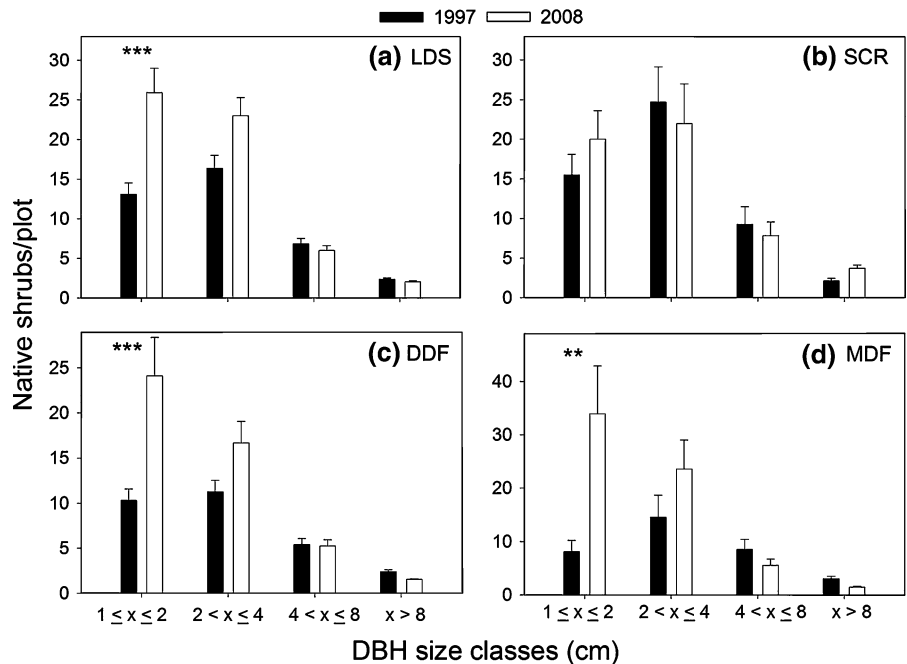
Relationship between native plant community structure, forest type, and lantana density

In 1997, species richness varied significantly with forest type ($F_{3, 126} = 2.96$, $P = 0.03$), but not with mean lantana density ($F_{1, 126} = 0.005$, $P = 0.94$; Table 5),

indicating that forest type differences, rather than lantana density was a better predictor of species richness. However, species richness was significantly affected by an interaction between forest type and lantana density ($F_{3, 126} = 3.69$, $P = 0.01$). Shannon's H' varied significantly with forest type ($F_{3, 126} = 3.02$,

Fig. 5 The mean number of
lianas in each size class per
plot, at the level of the
landscape (**a**) and at the
level of individual forest
types, scrub-savanna (**b**),
dry deciduous forest (**c**), and
moist deciduous forest (**d**) in
1997 and 2008. Note
differences in y-axis scale
among panels
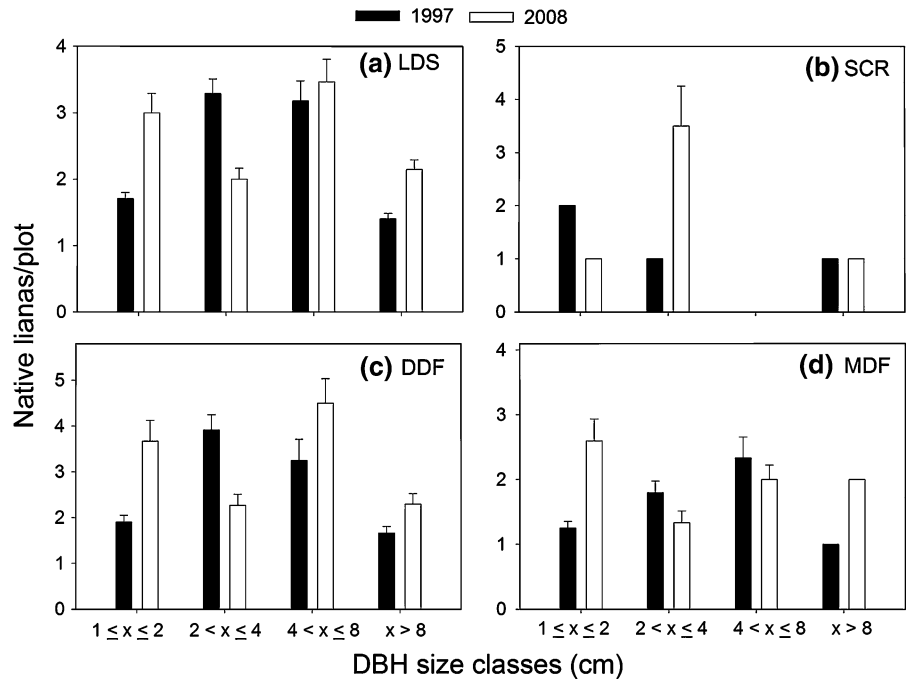
Table 5 Relationship between species richness, Shannon's H', and evenness J, as a response to forest type and lantana stems/plot in 1997 and 2008

Forest type	Response variable	Source of variation (P^a)			
		Forest type		Lantana stems/plot	
		1997	2008	1997	2008
Scrub-savanna	Species richness	*	ns	*	ns
	Shannon H'	ns	ns	ns	ns
	Evenness J	***	ns	ns	ns
Dry deciduous	Species richness	***	***	*	ns
	Shannon H'	***	***	ns	***
	Evenness J	***	***	ns	***
Moist deciduous	Species richness	**	*	**	ns
	Shannon H'	*	ns	**	ns
	Evenness J	ns	·	ns	ns
Evergreen	Species richness	*	**	ns	ns
	Shannon H'	*	**	ns	ns
	Evenness J	ns	ns	ns	ns

For the ANCOVA, forest type was the categorical predictor, and mean lantana stems/plot the independent covariate. The significance of the sources of variation within each forest type was determined using a post hoc Turkey's test

[a] Values of P are indicated by '***'($P < 0.0001$), '**' ($P < 0.001$), '*'($P < 0.05$), '·'($P < 0.1$) and ns (non-significant)

$P = 0.03$), and weakly significantly with mean lantana density ($F_{1, 126} = 3.25$, $P = 0.07$). Additionally, Shannon's H' was significantly affected by an interaction between forest type and lantana density ($F_{3, 126} = 2.83$, $P = 0.04$). Evenness J varied significantly with forest type ($F_{3, 126} = 5.37$, $P = 0.001$), and with

mean lantana density ($F_{1, 126} = 10.23$, $P = 0.001$). Evenness J was significantly, but weakly, affected by an interaction between forest type and lantana density ($F_{3, 126} = 2.29$, $P = 0.08$; Table 5) in 1997.

In 2008, species richness varied significantly with forest type ($F_{3, 114} = 4.08$, $P = 0.008$), but not with mean lantana density ($F_{1, 114} = 0.92$, $P = 0.34$; Table 5). Species richness was unaffected by an interaction between forest type and lantana density ($F_{3, 114} = 0.68$, $P = 0.56$). On the other hand, Shannon's H' varied significantly with forest type ($F_{3, 114} = 7.08$, $P = 0.0002$), and with mean lantana density ($F_{1,114} = 31.23$, $P < 0.0001$). However, Shannon's H' was unaffected by an interaction between forest type and lantana density ($F_{3, 114} = 0.53$, $P = 0.66$). Lastly, Evenness J varied significantly with forest type ($F_{3, 114} = 10.75$, $P < 0.0001$), and with mean lantana density ($F_{1, 114} = 111.45$, $P < 0.0001$). Similar to species richness and Shannon's diversity, Evenness J was unaffected by an interaction between forest type and lantana density ($F_{3, 114} = 0.14$, $P = 0.94$; Table 5).

Discussion

Invasive species spread and the invasibility of heterogeneous landscapes

In this study, even though the forest types differ in their physical structure, high levels of lantana invasion are seen in the deciduous forest types, which have an open canopy for up to 3 months of the year, as compared with the evergreen forest type. Canopy openness has been reported to be a key factor that influences lantana invasibility in many forest types across the world. In the wet, sclerophyllous forests of Australia, lantana invasion increases with understory and overstory canopy removal (Duggin and Gentle 1998). Similarly, studies in the dry forests of Uganda report that gap size and canopy openness are key factors that govern lantana population size and reproductive output (Totland et al. 2005). There is also evidence for lantana cover being much higher in areas with a low native canopy cover (Raizada et al. 2008). Canopies in the deciduous forests of BRT are largely leafless during February- March every year (R. Siddappa Setty, unpublished data). Canopy openness in the deciduous forest types could thus facilitate

the invasion of lantana in the deciduous forests of BRT by improving both its germination and reproduction (Day et al. 2003).

In addition to canopy openness, there could be other factors that enhance lantana success in BRT. There is evidence that seed germination and seedling establishment rates of lantana increase with light availability and disturbance such as fire and understory clearing (Duggin and Gentle 1998). There is also evidence that lantana exerts tremendous propagule pressure—particularly from invaded areas—that enables it to colonize uninvaded sites over time (Sundaram et al. unpublished manuscript). Therefore, habitat heterogeneity, combined with the proximity of lantana seed sources (i.e. sources of propagule pressure), may be playing a role in influencing ecosystem invasibility.

Invasive species spread and correlation with change in native plant communities

This study clearly shows that by 2008, the distribution and density of lantana has increased dramatically in BRT from its 1997 levels. Overall, the increase in lantana density has been the most in the deciduous forest types (scrub-savanna, dry-, and moist deciduous forests). Gooden et al. (2009a) found that native plant species richness, diversity, abundance, and population structure are negatively correlated with lantana invasion. Conversely, removing lantana from sites resulted in increased native species recruitment and richness, indicating that active management, including follow-up removals, can mitigate the negative effects of lantana invasion (Gooden et al. 2009a). Vegetation type heterogeneity has been found to influence levels of weed invasion in many areas, with some vegetation types like grasslands and lowlands being more prone to invasion than heathlands and uplands (Chytry et al. 2009; Stohlgren et al. 2002).

Lantana invasion in BRT has been accompanied by (though did not necessarily cause) significant reductions in native plant species richness, diversity and evenness, at both the landscape scale and in the deciduous forest types. Accurate identification of plant species in non-destructive plant ecological studies is extremely challenging when there are up to 158 species per vegetation type. Accordingly, the dramatic reduction in species richness (approximately 22% local extinction) may be more apparent than real, due

in part to the previous researchers (Murali and Setty 2001) identifying the native woody plants present as a greater number of species, or due to underestimation of species in the present study. Nonetheless, we do not think that the dramatic reduction in species richness (approximately 22% local extinction) observed in this study can be wholly attributed to discrepancies in species identification alone.

Although lantana was reported from BRT almost eight decades ago, lantana density was relatively negligible in 1997 when compared to 2008. The recent and rapid spread of lantana in BRT, despite its relatively long presence in the area, supports the idea of a lag phase in invasive species spread within heterogeneous habitats (Sakai et al. 2001). After arrival, invasive species are sometimes able to lie in wait for long periods of time before expanding their range or increasing in abundance (Wangen and Webster 2006; Crooks 2005; Shigesada et al. 1995).

The correlation of reducing native plant species richness, diversity, and evenness with increasing lantana density could possibly occur directly or indirectly. Sakai et al. (2001) broadly classify interactions between native and invasive species as either being direct (via predation or competition) or indirect (via habitat alteration). Community-level declines in species richness, diversity, and evenness observed in BRT indicate that both direct and indirect interactions may be occurring simultaneously. However, decreasing species richness and diversity along a lantana invasion gradient in BRT could have probably occurred due to direct effects of harvesting and herbivory, or indirectly due to the effect of disturbance such as fire, all eventually facilitating invasion by lantana. Some native species are probably being out-competed by lantana, possibly because lantana—like other invasive species—utilizes limiting resources efficiently (e.g. Funk and Vitousek 2007) and produces allelopathic chemicals (Day et al. 2003). Additionally, due to the stem-dominance of lantana in BRT, indirect effects on native species due to alteration of habitat are also possible. Indirect effects on native species may occur due to the shading and allelopathy of lantana causing poor germination and survival of light-demanding seedlings of native tropical dry forest species (Vieira and Scariot 2006) under conditions of high lantana abundance and shade.

Changes in the demography of native woody species

Invasive species affect native biodiversity by suppressing recruitment (Litton et al. 2006) and by changing the physical structure of invaded forests (Mason and French 2008). The size-class structure of trees and shrubs in BRT has changed simultaneously with the increase in lantana abundance. Lantana invasion is most likely resulting in recruitment limitation for small trees. In a heterogeneous landscape like BRT, examining the effects of lantana on size-class distributions at both the landscape scale and at the scale of individual forest types has proved to be useful.

The landscape-level patterns of size-class distributions in 1997 and 2008 indicate that recruitment limitation is occurring in all size classes of trees, suggesting not only a lack of regeneration, but also a lack of recruitment of smaller individuals into larger size classes. This is possibly due in part to the effects of herbivory and lopping of branches during the harvest of certain non-timber forest products (Sinha and Bawa 2002). This may also be due to fire—especially in lantana-invaded areas fires have been observed to cause mortality of large trees (Prasad 2009).

However, analysis of tree size-class distributions within each forest type revealed that the recruitment of small stems is more significantly affected than recruitment into larger size classes. This is so especially in the case of the scrub-savanna and dry deciduous forests. Lantana could impede the recruitment of young individuals by successfully competing for space and light through superior (hybrid) growth vigour, shading and allelopathy, which is a pattern that has been observed in Australia (Gooden et al. 2009a).This corroborates studies in a neighbouring tropical dry forest, which indicate that tree populations are bereft of saplings in lantana-invaded areas (Prasad 2010). Lastly, the reduction in the density of small, medium and especially adult trees in the moist deciduous forests is probably also due to the effects of other disturbances (such as harvesting, herbivory and fire) that occur in the study area (Duggin and Gentle 1998). Transformation of portions of twelve 4-km^2 grids of native forest into agricultural use and human habitation, especially expansion of the coffee plantations located in the core of the sanctuary,

between 1997 and 2008 (despite the notification of BRT as a wildlife sanctuary in 1973; Barve et al. 2005) may have increased the demand for firewood, and harvesting of native trees may not be completely prevented. Protection of wildlife in BRT (as intended by the creation of the sanctuary) may have resulted in increasing populations of the mammals mentioned, and thus increased their herbivory on native plants to a level that is damaging the native vegetation.

The frequency and intensity of forest fires in the tropical dry forests of the Western Ghats is on the increase (Kodandapani et al. 2004). It is also possible that fires occurring in areas heavily invaded by lantana are more intense (Hiremath and Sundaram 2005) with lantana possibly creating ladder fuels that lead to canopy fires (Tireman 1916). Prasad (2009) suggests that tree mortality is higher in areas with a dense lantana understory, especially along roads, when compared to areas free of lantana and away from roads. Therefore, the reduction in the population of small, medium and especially large trees in the moist deciduous forests of BRT may be due to the combined effects of increased harvesting, herbivory and forest fires facilitating the lantana invasion. The most striking apparent impact of the invading lantana is to reduce recruitment of seedlings of native plants in all forest types. However, more experimental work will be required to investigate the mechanistic links between reduced tree recruitment and lantana invasion.

Unlike the size-class distribution of trees, where recruitment limitations have been observed, lantana invasion has been accompanied by an increase in the density of juvenile shrubs at the landscape level. This was surprising, considering that lantana density was negatively correlated to tree cover in Australian rainforests (Fensham et al. 1994). Patterns of increased juvenile shrub recruitment seen at the landscape level have been mirrored by patterns observed in the dry- and moist deciduous forests. The increase in the density of small shrubs was largely driven by the recruitment of two species: *Maesa indica*, and *Cipadessa baccifera*. These two species are probably responding positively to the same factors that promote lantana. Both *M. indica* and *C. baccifera* share characteristics shown by lantana: both species are understory shrubs, have fruits that are bird dispersed, and are unpalatable to wild herbivores (M.D. Madhusudan, personal communication), implying that herbivores are probably having an impact on the survival of palatable native plants. The possible lack of dispersal limitation and possession of defence against herbivory may be contributing to the population increases of both *M. indica* and *C. baccifera*.

Changes in the species composition and population structure of trees and shrubs in BRT are likely to result in further changes in the physical structure of the forest over the long term. Recruitment limitations seen for tree populations in BRT are likely to be amplified over the long term, since there will be fewer recruits available to replace dying adult trees. Simultaneously, an increase in the population of shrubs such as *M. indica* and *C. baccifera* is likely to make the deciduous forests of BRT shrubbier than what they are presently. Community level changes that occur due to the effects of harvesting, herbivory, fire and invasive species often result in a shift in the physical structure of the forest. For example, lantana-invaded forests in Australia have shown a gradual shift in physical structure from tall woodland to short-statured shrubland (Gooden et al. 2009b). Results from this study indicate that active and large-scale lantana removal coupled with restoration efforts will be required to arrest and reverse the negative effects of lantana in the BRT landscape.

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