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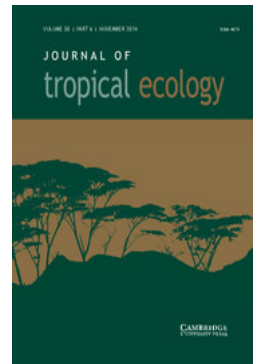
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# The association between invasive *Lantana camara* and seedlings/saplings of a plant community in Mudumalai Tiger Reserve, India

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**Abstract:** We examined changes in a community of seedlings/saplings 10–150 cm tall associated with the presence of a widely invasive plant, *Lantana camara* and environmental covariates along 67 randomly located transects, in Mudumalai, India. We compared plant species assemblage and grass cover in *L. camara*-invaded and uninvaded plots in three habitats. Multivariate analyses revealed a significant association of all environmental covariates with plant species assemblage. Pairwise tests indicated that *L. camara* was significantly associated with changes in plant species assemblage and grass cover within the moist and dry deciduous forest, but not in the thorn forest. The relationship between *L. camara* and that of elephant browse plants varied with species. A linear regression analysis indicated that *L. camara* invasion was the only significant predictor of grass occupancy. Our results indicate that in addition to other factors, *L. camara* was associated with altering plant species assemblage, some elephant browse plants and grass cover in the moist and dry deciduous forest. It appears that *L. camara* can have a major effect on diversity within this reserve, but whether this effect is by *L. camara* driving the change or being associated with other habitat change requires further experimental evidence.

**Key Words:** anthropogenic disturbance, elephants, grass cover, invasive weeds, *Lantana camara*, plant species assemblage

## INTRODUCTION

Exotic plant species may modify native communities by altering soil properties such as nutrient cycling (Ehrenfeld *et al.* 2001), hydrology (Melgoza *et al.* 1990), be allelopathic (Gentle & Duggin 1997a), or compete with native species for light and nutrients (Braithwaite *et al.* 1989, Woods 1993). Native forage species used by herbivores as food may therefore receive only limited resources due to competition with exotic plants, thus causing native species to become locally extinct or to persist at very low densities (Bedunah 1992). Changes to the vegetation community through a decline of native forage species brought about by exotic weeds could have the potential to precipitate food-web-level, bottom-up meltdown (*sensu* Terborgh *et al.* 2001).

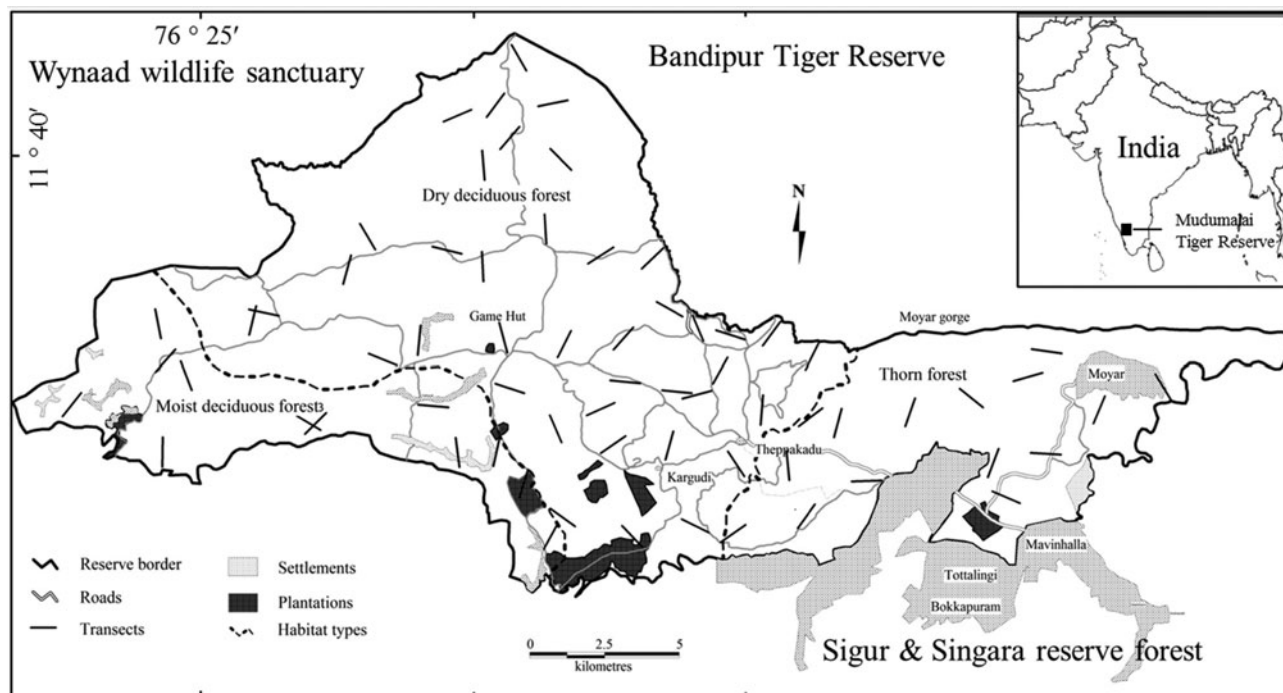
Exotic plants often require some form of disturbance for them to establish (Buckley *et al.* 2007, Duggin & Gentle 1998). In addition to the impact of exotic plant

invasions on native plant communities, a number of studies have shown that anthropogenic disturbances can also alter plant communities (Godefroid & Koedam 2004). Biotic factors such as tree density, canopy cover, grass cover and abiotic factors such as fire, distance to roads and settlements are also responsible for changes to the vegetation community (Morrison *et al.* 1995, Oliveira-Filho *et al.* 1998).

Megaherbivores such as the Asian elephant (*Elephas maximus*) are adapted to live in diverse habitats and feed on a variety of plant species (Baskaran *et al.* 2010, Owen-Smith 1988). However, despite their ability to exploit a wide range of forage species, elephants may be influenced by the establishment and spread of exotic invasive plants especially if these exotic plants are not eaten by elephant and replace native forage species (Wilson *et al.* 2014). The establishment of exotic invasive plants often leads to displacement and decline of native forage species (Lym & Kirby 1987).

Mudumalai Tiger Reserve (hereafter Mudumalai) in southern India forms a part of the Nilgiri Biosphere Reserve which hosts the single largest Asian elephant

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**Figure 1.** Mudumalai Tiger Reserve and its location in India showing the layout of 67 transects across the reserve within the three habitats. Habitat boundaries are delimited by dashed lines: moist deciduous, dry deciduous and thorn forest. Plantations are shown as black patches and settlements as grey patches. The road network within the reserve is shown.

population. In Mudumalai, one study estimates that browse forms 15% of elephant diet while grass forms nearly 85% of elephant diet (Baskaran *et al.* 2010). One of the physical impacts *Lantana camara* L. has is the reduction of grass cover. As *L. camara* spreads, grass cover declines (Kumar *et al.* 2012). This reduction in major elephant food source could lead to detrimental effects on elephants and their habitats (Prasad 2012). For large herbivores, whose populations are not regulated through natural predation, it is likely that the availability of food is the limiting resource (Owen-Smith 1988, Sinclair 1975). Thus food resources are vital to maintaining elephant health and abundance.

*Lantana camara* has invaded India's tropical dry forests and appears to be associated with a reduction in food species of native herbivores (Prasad 2012). Elsewhere, sites invaded by *L. camara* generally have lower plant species richness and diversity (Prasad 2010, Sharma & Raghubanshi 2007), and the weed is also thought to impede the growth of grass and native seedlings (Gooden *et al.* 2009, Kumar *et al.* 2012). For these reasons, many reserves manage habitat by investing resources in *L. camara* removal, especially by cutting and uprooting plants (Srivastava 2009). We tested the hypotheses that *L. camara*, along with other biotic and abiotic environmental covariates was significantly associated with (1) plant species assemblage, (2) three elephant browse plants present throughout the reserve in a plant community

of seedlings/saplings 10–150 cm tall and (3) grass cover. Grass cover was examined because of the importance of grass in elephant diet (Baskaran *et al.* 2010, Wilson *et al.* 2014). We use the term 'association' here because this study was not a manipulative experiment.

## METHODS

### Study site and sampling design

The study was conducted in Mudumalai Tiger Reserve (Figure 1) southern India. Data were collected from  $10 \times 1$ -m plots located every 100 m along 67 1-km long randomly located transects as described by Wilson *et al.* (2013). The  $10 \times 1$ -m sampling plots located every 100 m were spaced in an attempt to ensure that the plots along each transect were independent given the size of the plots and the gap between each plot.

We first recorded *L. camara* presence or absence within each  $10 \times 1$ -m plot along each transect to examine changes that were associated with differences in plant species assemblage and grass cover. We were also interested in whether the abundance of *L. camara* in a plot was associated with differences in three elephant browse plant species. To measure *L. camara* abundance, stem density of *L. camara* in each plot was recorded. To estimate *L. camara* invasion, the age of the stand, defined by average

*L. camara* girth of all stems in a plot, was used because in field observations we noted that older stands had fewer *L. camara* plants (as few individuals dominate while others die out) as has been noted elsewhere (Swarbrick *et al.* 1998). By contrast, younger stands had more individual plants. The girth of all *L. camara* stems were measured at ground level within 10 × 1-m plots and recorded in 1-cm categories. An estimate of the average girth for each plot was derived.

Plant species (shrubs and saplings, between 10 and 150 cm) were identified from herbarium specimens, field guides and knowledgeable field assistants and counted in plots measuring 10 × 1-m located every 100 m along each transect in order to measure plant species assemblage at each plot (see Appendix 1 for a list of plant species). Biotic and abiotic environmental covariates that could potentially be associated with plant species assemblage were measured in each plot. Biotic covariates included tree density, canopy cover and grass cover. Tree density, canopy cover and percentage grass cover along each 1-km transect was estimated every 100 m in 10 × 1-m plots (Wilson *et al.* 2013). All grasses were grouped together without distinguishing the various species. The percentage of bare ground, other vegetation (trees, herbs, shrubs) and rocks, was also visually estimated at the same site. The percentage of grass occupancy (area of grass cover/area available to grass after deducting native vegetation, bare ground and rocks) was also calculated to provide a measure of the area in a plot that was actually occupied by grass or *L. camara*.

Abiotic environmental covariates related to anthropogenic disturbances and included distance to roads and settlements, and time since last fire burn. Linear distances between each sampling plot and the closest road and settlement were measured from 1:50 000 topographic maps, using MapInfo Professional 7.8 (MapInfo Corporation, Troy, NY, USA). As the size and thus potential impact of roads and settlements varied throughout Mudumalai, we used three categorical factors for settlements: (1) if a plot fell more than 2 km from a minor settlement ( $\leq 0.1$  km<sup>2</sup>); (2) if a plot fell within 2 km from a minor settlement; and (3) if a plot fell within 2 km of a major settlement ( $\geq 0.1$  km<sup>2</sup>). Similarly, for roads: (1) if a plot fell more than 2 km from a forest road (grey lines, Figure 1); (2) if a plot fell within 2 km from a forest road (grey lines, Figure 1); and (3) if a plot fell within 2 km of a main/public road (grey double lines, Figure 1). Within Mudumalai, smaller forest roads that were used only by the forest department's tourist vehicles were assumed to have less impact than the main/public road and were presumed to have minimal impact on weed distribution. Data on anthropogenic fire during the 6 y prior to the study (2003–2008) in each plot were obtained using the same methods described by Wilson *et al.* (2013).

## Statistical analyses

To assess differences in plant species assemblage in plots that were invaded and uninvaded by *L. camara* including environmental covariates, we used PERMANOVA+ using 9999 permutations implemented in PRIMER v 6.1.11 (Clarke & Gorley 2006). Only shrubs and saplings measuring between 10 and 150 cm in height were used. *Lantana camara* was excluded from the analysis of plant species assemblage, and was used only to define invaded/uninvaded groups. The data were log-transformed ( $\log(x + 1)$ ) prior to analyses. A Bray–Curtis index was used as a similarity measure for plant species assemblage (Clarke & Warwick 2001). We used non-metric Multi-Dimensional Scaling (nMDS), also implemented in PRIMER to determine whether plant species assemblage differed in the three habitats of the reserve. The nMDS was run over 1000 iterations using Kruskal stress formula 1 and a minimum stress of 0.01. To investigate the association of *L. camara* presence/absence with plant species assemblage further, we examined the output of PERMANOVA which includes pairwise tests within each habitat comparing plots with and without *L. camara*. The pairwise tests were conducted by including each habitat as a factor and *L. camara* presence/absence as a second factor. We were therefore able to define the association of *L. camara* within each habitat without analysing the data habitat-wise. As there were a large number of potential interactions between various factors, we a priori decided to examine only the interaction between habitat and *L. camara* presence/absence.

In order to examine how individual species contributed to the differences in plant species assemblage between *L. camara*-invaded and uninvaded plots, we used SIMPER subroutine (analysis of per cent similarity) (PRIMER v 6.1.11) based on a Bray–Curtis similarity measure, with a log-transformation of the data ( $\log(x + 1)$ ). The top three elephant browse food plants (saplings between 10–150 cm tall) that contributed most to the dissimilarity from the SIMPER analysis were then used to examine the slope of the relationship with *L. camara* abundance using linear regression analysis conducted in SPSS Statistics, release version 20.0 (IBM SPSS Inc., Chicago, IL, USA). The effect size of *L. camara* on each of the species that contributed to the average dissimilarity among habitats and between invaded and uninvaded plots, were derived using 'adonis' function in the 'vegan' package in R (version 3.0.2; <http://www.R-project.org>).

Given the importance of grass in elephant diet (Baskaran *et al.* 2010, Wilson *et al.* 2014), we conducted an analysis on percentage grass cover to study the association of *L. camara* and other environmental covariates with percentage grass cover. A Bray–Curtis index was used as a similarity measure for percentage grass cover. PERMANOVA+ was used to run 9999

permutations to test for an association of *L. camara* presence/absence and environmental covariates (biotic and abiotic) with percentage grass cover. Biotic and abiotic factors used as environmental covariates were *L. camara* presence/absence, tree density, canopy cover, impact of roads, settlements and fire. PERMANOVA was used to conduct pairwise tests to compare plots with and without *L. camara* within each habitat to examine these differences. As above, only interactions between habitat and *L. camara* presence/absence were examined and not all factor interactions.

A linear regression analysis was then conducted on percentage grass occupancy (defined as given above), to test for an association of *L. camara* invasion (average girth per plot) along with other environmental covariates, which included impact of roads, settlements, canopy cover, fire, tree density, DDF  $\times$  *L. camara* interaction and MDF  $\times$  *L. camara* interaction term with the percentage grass occupancy using SPSS Statistics, release version 20.0 (IBM SPSS Inc., Chicago, IL, USA). The TF was used as the reference category for the dummy variable and hence its interaction term with *L. camara* was not included in the model. Percentage grass occupancy per plot which was the outcome variable was arcsine-square root transformed for normality.

## RESULTS

*Lantana camara* has invaded large areas of Mudumalai. Overall, 59% of the sampling plots ( $n = 737$ ) were invaded by *L. camara* throughout the reserve. The thorn forest (TF) ( $n = 165$ ) had more *L. camara*-invaded sampling sites than the other habitats with 88% of sites invaded by *L. camara*. Of the sites sampled in the moist deciduous forest (MDF) ( $n = 132$ ), 43% remained uninvaded while 52% in the dry deciduous forest (DDF) ( $n = 440$ ) were uninvaded by *L. camara*. The density of *L. camara* varied throughout the reserve in different habitats from no *L. camara* to

39 stems per  $10 \times 1$ -m plot with an interquartile range of 4 stems per  $10 \times 1$ -m plot (25th percentile = 0 stems; 75th percentile = 4 stems). Of the 737 plots, only seven plots had no plants because they were occupied by bare earth or rock or by trees, while other plots had between 1 and 53 plant species. The total number of plant species identified within the plots throughout the reserve was 136 with *Catunera gum spinosa* (Rubiaceae) being the most common species (340 individuals). Plant species richness was highest in two plots along two different transects with a total of 53 plant species; one of these transects was found in the DDF while the other in the MDF.

### Plant species assemblage

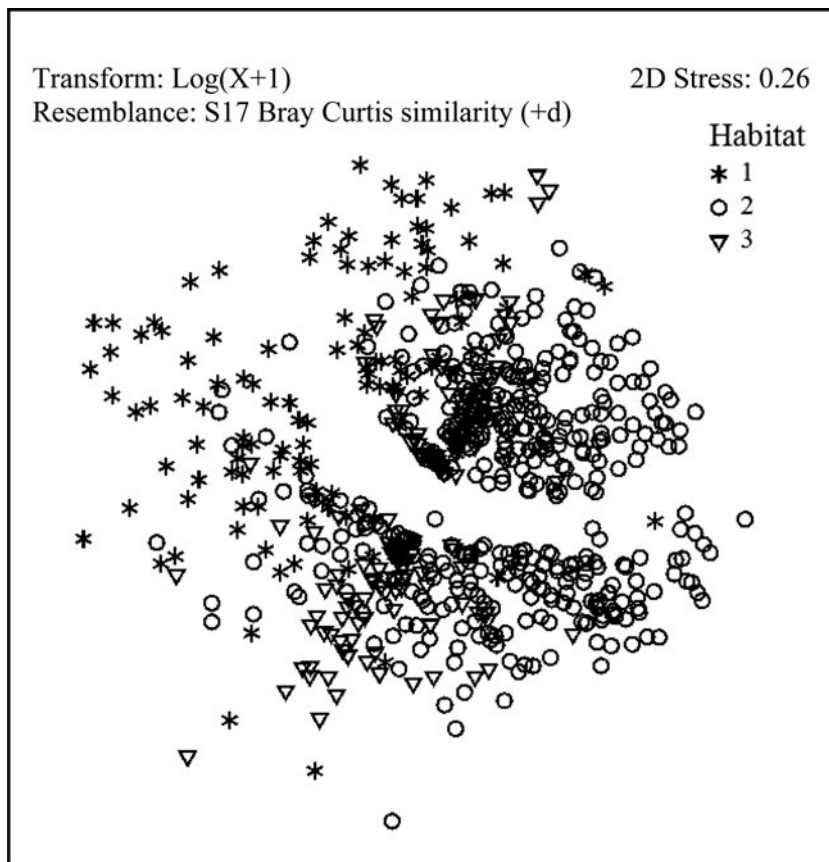
All environmental covariates, including the presence of *L. camara* in a plot were associated with the plant species assemblage ( $P < 0.001$ , Table 1). The largest component of variation was from habitat (14%), followed by *L. camara* presence/absence and roads (each 8%), settlements and the interaction of habitat and *L. camara* presence/absence (7%). The lowest component of variation was tree density (2%). Pairwise tests indicated that in both the MDF ( $t_{123} = 1.51$ ,  $P = 0.006$ ) and DDF ( $t_{430} = 4.39$ ,  $P < 0.001$ ), the presence of *L. camara* was significantly associated with differences in plant species assemblage, while there were no significant differences in the TF ( $t_{157} = 1.13$ ,  $P = 0.238$ ) whether *L. camara* was present or not. Two-dimensional nMDS plot did not reveal clear differences in plant species assemblage in the three habitats, perhaps related to the poor fit of the data to a two-dimensional nMDS plot (Stress  $> 0.20$ , Figure 2).

### Elephant browse plants

SIMPER analysis indicated that *C. spinosa* contributed 12.1% to the average similarity between habitats and

**Table 1.** Results of PERMANOVA (permutation analysis of variance) examining the association of *Lantana camara* presence/absence and environmental covariates with plant species assemblage in Mudumalai Tiger Reserve, India. All environmental covariates were statistically significant. PERMANOVA also gives a component of per cent variation for each predictor which is equivalent to the sum of the squared fixed effects divided by the degrees of freedom from standard ANOVA.

Environmental covariates	df	Pseudo-F	P(perm)	Estimate	Per cent variation
Habitat	2	20.7	<0.001	265.2	13.6
<i>Lantana camara</i> (presence/absence)	1	14.7	<0.001	93.2	8.1
Roads	2	7.8	<0.001	87.4	7.8
Settlements	2	5.8	<0.001	70.7	7.0
Habitat $\times$ <i>Lantana camara</i> (presence/absence)	2	3.0	<0.001	59.5	6.5
Fire	1	18.8	<0.001	54.9	6.2
Canopy cover	1	19.7	<0.001	53.5	6.1
Grass cover	1	9.1	<0.001	23.4	4.0
Tree density	1	3.8	<0.001	8.1	2.4
Residuals	723			2110.9	38.4
Total	736				



**Figure 2.** A non-metric Multi-Dimensional Scaling (nMDS) plot generated in PRIMER v 6.1.11 showing the dissimilarities of the various species in the three habitats of Mudumalai Tiger Reserve. The two-dimensional nMDS plot shows that there is a high stress level (0.26) which is higher than the maximum stress level of 0.20. Given the high stress level and the poor representation of the data which is highly distorted we abandoned the nMDS. The three habitats are (1) moist deciduous forest represented by a star, (2) dry deciduous forest represented by a hollow circle and (3) thorn forest represented by a triangle.

between plots with and without *L. camara*, followed by *Phyllanthus emblica* (Phyllanthaceae) (7.3%), *Shorea roxburghii* (Dipterocarpaceae) (5.7%), *Cassia fistula* (5.1%) and *Grewia tiliifolia* (Malvaceae) (4.5%) (Table 2). All these plants except for *C. fistula* are elephant browse food plants and the most important species in differentiating those plots with and without *L. camara*. Of the browse species that were estimated to contribute most to elephant diet by Baskaran *et al.* (2010), bamboo spp. (Gramineae) and *Kydia calycina* (Malvaceae) contributed only 3% to the average similarity, and only bamboo spp. were found in all three habitats.

The association between *L. camara* presence/absence and *C. spinosa* in the MDF was significant (MDF:  $t_{130} = -2.38$ ,  $P = 0.019$ ), while there was no significant association between *L. camara* presence/absence and *C. spinosa* in the DDF ( $t_{438} = -0.38$ ,  $P = 0.703$ ) or TF ( $t_{163} = -1.09$ ,  $P = 0.276$ ) (Figure 3a). However, *L. camara* abundance was negatively associated with *C. spinosa* in the DDF only ( $t_{438} = -2.93$ ,  $P = 0.004$ ). *Lantana camara* presence/absence was significantly associated with

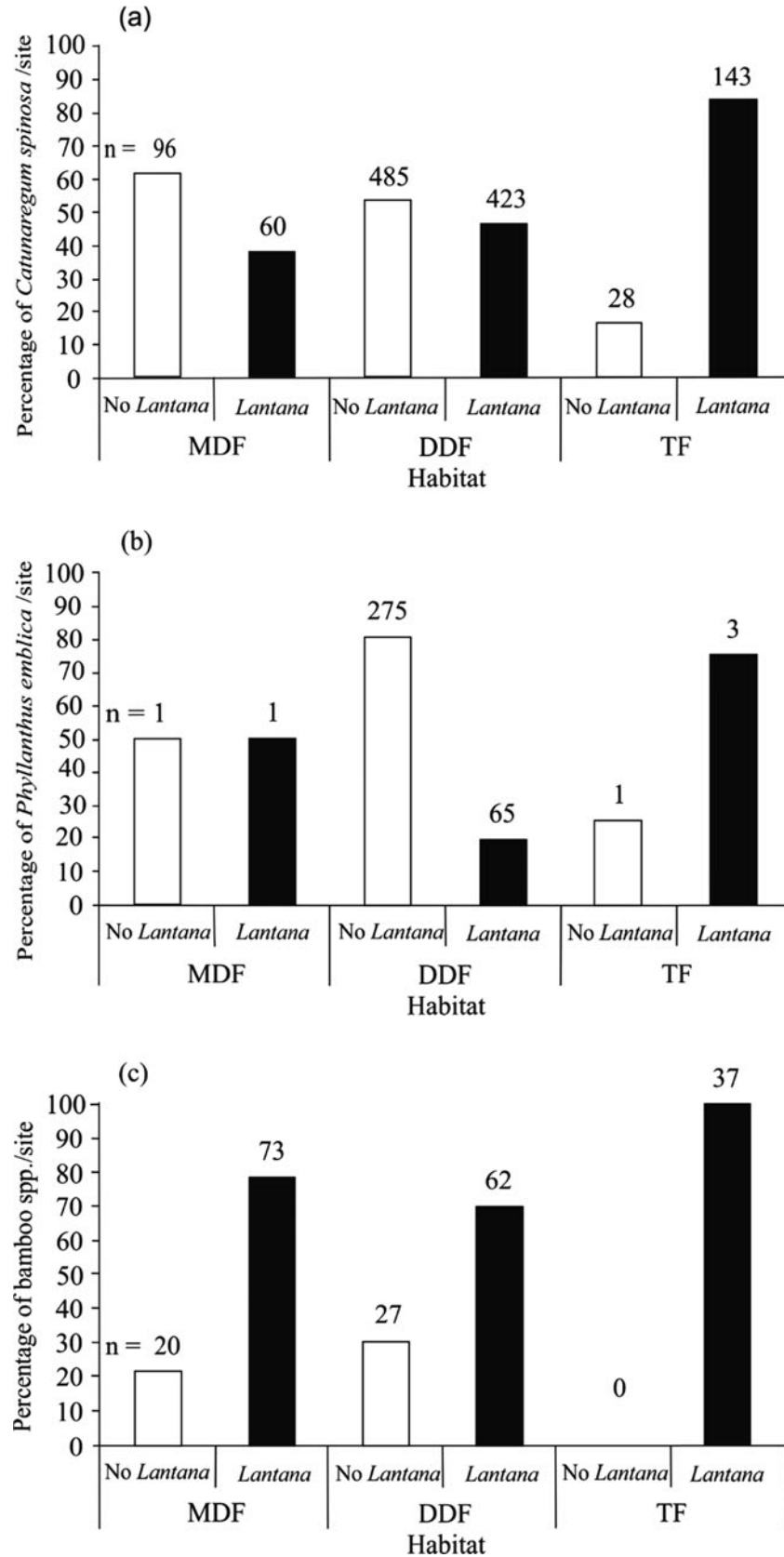
*P. emblica* in the DDF ( $t_{438} = -8.09$ ,  $P < 0.001$ ), but not in the MDF ( $t_{130} = 0.20$ ,  $P = 0.846$ ) or TF ( $t_{163} = 0.80$ ,  $P = 0.427$ ) (Figure 3b). *Shorea roxburghii* was present only in the DDF, but was absent in the MDF and TF. *Lantana camara* presence/absence was significantly associated with *G. tiliifolia* in the DDF ( $t_{438} = -2.48$ ,  $P = 0.014$ ), but not in the MDF ( $t_{130} = 1.35$ ,  $P = 0.180$ ) or TF ( $t_{163} = 1.34$ ,  $P = 0.184$ ). *Lantana camara* presence/absence was significantly associated with bamboo spp. in the MDF ( $t_{130} = 2.56$ ,  $P = 0.012$ ), but not in the DDF ( $t_{438} = 1.91$ ,  $P = 0.057$ ) or TF ( $t_{163} = 1.19$ ,  $P = 0.235$ ) (Figure 3c).

#### Percentage grass cover and occupancy

The PERMANOVA analysis indicated that percentage grass cover differed significantly according to whether a plot was invaded or uninvaded by *L. camara* ( $P < 0.001$ , Table 3). In fact, the highest component contributing to the variation was *L. camara* presence/absence (16%), followed by the interaction term between habitat and

**Table 2.** Results of the SIMPER analysis showing the relative and cumulative contributions of various species that contributed to 90.05% of the average dissimilarity among habitats and between invaded and uninvaded plots in Mudumalai Tiger Reserve, India. The effect of *Lantana camara* on each of these species is shown as coefficients. Elephant browse food species are indicated with an asterisk.

Species	Average bundance		Average dissimilarity	%		
	Invaded	Uninvaded		Contribution	Cumulative	Coefficient
* <i>Catunaregum spinosa</i>	0.56	0.69	11.1	12.2	12.2	-0.025
* <i>Phyllanthus emblica</i>	0.09	0.46	6.66	7.32	19.5	-0.004
* <i>Shorea roxburghii</i>	0.04	0.35	5.18	5.69	25.2	-0.005
<i>Cassia fistula</i>	0.20	0.18	4.64	5.09	30.3	-0.005
* <i>Grewia tiliifolia</i>	0.16	0.25	4.11	4.51	34.8	0.007
* <i>Kydia calycina</i>	0.11	0.18	3.03	3.33	38.1	-0.001
* <i>Bambusa arundinacea</i>	0.18	0.07	2.67	2.93	41	-0.001
<i>Glycosmis pentaphylla</i>	0.14	0.13	2.64	2.9	43.9	0.004
* <i>Tectona grandis</i>	0.11	0.10	2.6	2.86	46.8	0.001
<i>Anogeissus latifolia</i>	0.02	0.20	2.4	2.64	49.4	0.000
* <i>Diospyros montana</i>	0.10	0.10	2.19	2.41	51.8	0.004
* <i>Dalbergia latifolia</i>	0.10	0.10	2.13	2.34	54.2	0.003
* <i>Grewia hirsuta</i>	0.09	0.07	1.81	1.98	56.2	0.003
* <i>Helicteres isora</i>	0.08	0.08	1.57	1.73	57.9	-0.004
* <i>Olea dioica</i>	0.04	0.10	1.46	1.61	59.5	0.000
* <i>Syzygium cumini</i>	0.07	0.07	1.44	1.58	61.1	-0.003
* <i>Desmodium pulchellum</i>	0.05	0.09	1.42	1.56	62.6	-0.002
* <i>Ziziphus oenoplia</i>	0.06	0.03	1.42	1.56	64.2	0.002
<i>Terminalia crenulata</i>	0.00	0.10	1.3	1.43	65.6	0.002
* <i>Schleichera oleosa</i>	0.06	0.04	1.24	1.36	67.1	0.005
* <i>Pterocarpus marsupium</i>	0.02	0.08	1.18	1.3	68.3	0.000
<i>Dalbergia lanceolaria</i>	0.05	0.05	1.11	1.22	69.51	-0.003
<i>Opuntia</i> spp.	0.06	0.01	1.01	1.11	70.7	-0.001
Zingiberaceae	0.11	0.00	0.98	1.07	71.7	-0.004
<i>Casearia esculenta</i>	0.03	0.09	0.97	1.07	72.8	0.000
<i>Cordia wallichii</i>	0.04	0.03	0.89	0.98	73.8	0.001
<i>Canthium dicoccum</i>	0.05	0.03	0.76	0.84	74.6	-0.001
<i>Cinnamomum malabathrum</i>	0.02	0.06	0.71	0.78	75.4	-0.001
<i>Coffea robusta</i>	0.03	0.06	0.66	0.73	76.8	-0.001
<i>Olea glandulifera</i>	0.01	0.07	0.66	0.72	77.6	0.001
<i>Cassia tora</i>	0.05	0.01	0.64	0.7	78.3	-0.003
<i>Cipadessa baccifera</i>	0.04	0.03	0.6	0.66	78.9	-0.002
* <i>Ziziphus xylopyrus</i>	0.04	0.01	0.58	0.64	79.6	-0.001
* <i>Terminalia tomentosa</i>	0.00	0.06	0.57	0.62	80.2	0.000
<i>Ougeinia oojenensis</i>	0.01	0.04	0.56	0.61	80.8	0.002
<i>Murraya paniculata</i>	0.01	0.05	0.54	0.59	81.4	0.002
* <i>Albizia lebbek</i>	0.01	0.03	0.5	0.55	81.9	0.000
<i>Zizyphus rugosa</i>	0.02	0.01	0.48	0.53	82.5	0.001
* <i>Solanum torvum</i>	0.03	0.01	0.48	0.53	82.9	0.003
* <i>Acacia</i> spp.	0.04	0.02	0.48	0.52	83.5	0.003
<i>Lagerstroemia microcarpa</i>	0.03	0.01	0.47	0.52	84	0.000
<i>Urena lobata</i>	0.03	0.02	0.46	0.51	84.5	0.000
<i>Argeratum conyzoides</i>	0.01	0.01	0.43	0.47	85	0.001
<i>Maytenus emarginata</i>	0.03	0.01	0.43	0.47	85.5	0.001
<i>Flueggea leucopyrus</i>	0.02	0.01	0.43	0.47	85.9	-0.001
* <i>Solanum auriculatum</i>	0.03	0.01	0.42	0.46	86.4	0.001
<i>Viburnum punctatum</i>	0.01	0.04	0.4	0.44	86.8	0.000
* <i>Acacia leucophloea</i>	0.02	0.00	0.39	0.43	87.3	-0.002
<i>Persea macrantha</i>	0.01	0.04	0.38	0.42	87.7	0.001
<i>Terminalia chebula</i>	0.01	0.03	0.38	0.42	88.1	0.000
<i>Erythroxylum monogynum</i>	0.02	0.01	0.38	0.42	88.5	0.000
<i>Argyrea cuneata</i>	0.00	0.02	0.36	0.39	88.9	0.000
* <i>Tamilnadia uliginosa</i>	0.01	0.03	0.34	0.37	89.3	0.000
<i>Actinodaphne malabarica</i>	0.01	0.02	0.32	0.35	89.7	-0.001
<i>Sterculia guttata</i>	0.00	0.03	0.32	0.35	90	0.000
<i>Naringi crenulata</i>	0.01	0.01	0.31	0.34	90.3	-0.001



**Figure 3.** Relative abundance of three plant taxa important for elephant food, in invaded and uninvaded plots in the three habitats. These plants were selected from the SIMPER analysis *Catunaregum spinosa* (a), *Phyllanthus emblica* (b) and bamboo spp. (c) in *Lantana camara* invaded and uninvaded plots in three habitats (moist deciduous forest (MDF); dry deciduous forest (DDF) and thorn forest (TF)) of Mudumalai Tiger Reserve, India. Numbers above the bars refer to the number of individual plants of each species in each habitat.

**Table 3.** Results of PERMANOVA (permutational analysis of variance) examining the association of *Lantana camara* presence/absence and environmental covariates on percentage grass cover in Mudumalai Tiger Reserve, India. The component of per cent variation (equivalent to the sum of squared fixed effects divided by the degrees of freedom from standard ANOVA) for each predictor is given. All environmental covariates except for tree density were significant predictors of percentage grass cover.

Environmental covariates	df	Pseudo-F	P(perm)	Estimate	Per cent variation
<i>Lantana camara</i> (presence/absence)	1	43.3	<0.001	70.0	15.6
Habitat × <i>Lantana camara</i> (presence/absence)	2	6.8	0.001	43.2	12.3
Roads	2	5.9	0.002	15.6	7.4
Habitat	2	4.6	0.008	12.0	6.5
Settlements	2	3.9	0.015	10.7	6.1
Canopy cover	1	6.6	0.008	3.9	3.7
Fire	1	5.9	0.012	3.7	3.6
Tree density	1	3.0	0.086	1.5	2.3
Residuals	724			523.0	42.7
Total	736				

**Table 4.** Results of the linear regression of environmental covariates including *Lantana camara* invasion (average girth per plot) predicting percentage grass occupancy in Mudumalai Tiger Reserve, India. *Lantana camara* invasion was the only significant predictor of percentage grass occupancy. The interaction terms, moist deciduous forest (MDF) and dry deciduous forest (DDF) with *L. camara* are included in the model. The interaction term thorn forest (TF) and *L. camara* was set to zero because of redundancies in the model.

Environmental covariates	Coefficients		Beta	t	P
	Unstandardized	Standardized			
	B	SE			
(Constant)	77.8	4.5		17.3	<0.001
<i>Lantana camara</i>	− 1.8	0.5	− 0.2	− 3.7	<0.001
Canopy cover	− 0.1	0.0	− 0.1	− 1.8	0.065
Fire	− 0.2	0.8	0.0	− 0.2	0.841
Tree density	− 5.9	22.5	0.0	− 0.3	0.795
Roads	− 0.2	1.9	0.0	− 0.1	0.926
Settlements	− 2.3	2.1	− 0.1	− 1.1	0.265
MDF × <i>Lantana camara</i>	− 0.8	0.6	− 0.1	− 1.3	0.184
DDF × <i>Lantana camara</i>	− 0.5	0.9	0.0	− 0.6	0.559

*L. camara* presence/absence (12%), and roads (7%). Tree density was not a significant predictor of percentage grass cover ( $P = 0.086$ ). However, all other environmental covariates were significantly associated with percentage grass cover ( $P < 0.015$ , Table 3). Pairwise tests indicated that percentage grass cover significantly differed in the MDF ( $t_{120} = 3.51$ ,  $P = 0.003$ ) and DDF ( $t_{424} = 1.97$ ,  $P = 0.034$ ) depending on whether *L. camara* was present or absent. However, the presence of *L. camara* made no difference to the percentage grass cover in the TF ( $t_{153} = 0.80$ ,  $P = 0.441$ ). Thus it is difficult to generalize on the common effects of *L. camara* across the different habitats.

The linear regression of the *L. camara* invasion (average girth per plot) and environmental covariates on percentage grass occupancy across habitats was statistically significant, although explained only a small amount of variation ( $F_{8, 736} = 6.7$ ,  $R^2 = 0.07$ ,  $P < 0.001$ ). *Lantana camara* invasion was the only significant predictor of the percentage grass occupancy ( $P < 0.001$ , Table 4), possibly indicating competition for the same space. There was a significant negative correlation between percentage

grass occupancy and *L. camara* in all three habitats, indicating that as *L. camara* invasion increased, grass occupancy declined.

## DISCUSSION

Our results indicate a significant association between *L. camara* and a change in plant species assemblage, some elephant browse plants, percentage grass cover and occupancy in the moist and dry deciduous habitats of Mudumalai, but not in the thorn forest.

### Plant species assemblage

While the three habitats in Mudumalai are clearly different in terms of their plant species assemblage, PERMANOVA pairwise tests of the interaction between habitat and plots with and without *L. camara* indicated that *L. camara* presence/absence made a significant

difference only to the moist deciduous forest (MDF) and dry deciduous forest (DDF) of Mudumalai and not the thorn forest. In the MDF, 43% of the sampled sites had *L. camara* present while in the DDF, 48% of the sampled sites were invaded by *L. camara*. The MDF has the highest shrub and sapling density and diversity compared with the DDF and thorn forest (TF) in Mudumalai (Kumar 2011). It is likely that *L. camara* is capable of changing the diversity and density of shrubs and saplings and hence we see an association of *L. camara* in the MDF because of the higher diversity and density of shrubs and saplings. The MDF is a closed-canopy forest and closed canopy is known to hamper *L. camara* growth (Duggin & Gentle 1998, Fensham *et al.* 1994). However, *L. camara* was recognized as a problem taking over the understorey and spreading rapidly in the Benne and Mudumalai blocks of the MDF and affecting the growth rate of teak in its early stages as early as 1924 in Mudumalai when timber extraction was carried out (Ranganathan 1941). The timber extractions may have opened up the canopy and facilitated *L. camara* invasion suggesting that *L. camara* may be the 'passenger' here, but further studies are required to confirm its role here. Nevertheless, *L. camara* has contributed significantly to a change in the plant species assemblage in the MDF.

Similarly, there was an association between *L. camara* presence and plant species assemblages in the DDF, where timber extraction continued until a ban on logging in the 1980s (Srivastava 2009). Anthropogenic disturbances such as logging may have opened up the canopy which has increased the amount of light penetrating into the forest floor. Opening up of the forest canopy and allowing more light, however, is an advantage to exotic invasive species such as *L. camara* that are known to germinate with an increase in light availability (Gentle & Duggin 1997b, Totland *et al.* 2005). Anthropogenic disturbances have also been known to facilitate exotic plant invasions (Buckley *et al.* 2007, Duggin & Gentle 1998) and may have facilitated *L. camara* invasion here.

In addition to logging, fire has also been regarded as having a major impact on native sapling regeneration in the DDF (Sivaganesan & Sathyanarayana 1995). Fires have been shown to facilitate the spread of *L. camara* elsewhere (Hiremath & Sundaram 2005). Fires suppress native saplings and facilitate germination and spread of *L. camara* (Berry *et al.* 2011, Raizada & Raghubanshi 2010) in the DDF. It is likely that the association of *L. camara* with plant species assemblage is seen in the DDF because of the impact of logging and fire in the DDF. Grasses can be fuel loads that influence fire frequency and intensity (Scholes & Archer 1997). In the MDF, however, fire has been suggested to have much less impact on native species regeneration because grasses in the MDF retain their moistness even in the dry season, which reduces fire frequency and intensity (Sivaganesan 1991). In the TF, a lack of litter accumulation and cattle grazing

results in reduced fire frequency and intensity (Daniel *et al.* 1995, Sivaganesan 1991). However, when interpreting the response of native species distribution and abundance to infestations of exotic plants, caution must be exercised because infrequent plants may just be rare because of their nature of being rare, or may have been displaced by weed invasions (Butler & Cogan 2004).

In addition to *L. camara*, the results of our study also show that biotic and abiotic environmental covariates such as tree density, canopy cover, grass cover, impact of roads, settlements and fire are also significantly associated with plant species assemblage. Elsewhere, the association of environmental covariates with plant species assemblage have also been documented indicating the role that biotic and abiotic factors have in the floristic assemblage. For example, Angold (1997) investigated the effect of a road on adjacent heathland vegetation in the UK, and found that there was an increase in the abundance of grasses in the vegetation near the road. In Australia, fire frequency was estimated to account for 60% of the floristic variation (Morrison *et al.* 1995). In a central Brazilian deciduous dry forest, plant species abundance and distribution was significantly correlated with canopy gaps (Oliveira-Filho *et al.* 1998). Thus, other environmental covariates are also responsible for changes in the plant community.

### Elephant browse plants

Plant species are likely to respond to *L. camara* invasion differently, depending on different stages of its invasion (Gooden *et al.* 2009). While some native species are excluded more easily than others from invaded communities, the resistance of native species to invasion varies (Standish *et al.* 2001). For example, *C. spinosa* that forms only 0.15% of elephant diet in Mudumalai (Baskaran *et al.* 2010) was significantly associated with the presence of *L. camara* only in the MDF, but not in the DDF and TF, while the slope of the relationship between *L. camara* abundance and *C. spinosa* was negative only in the DDF and not in the MDF or TF. Further, bamboo spp. did not appear to be associated with *L. camara* presence in the DDF and TF but was significantly associated with *L. camara* presence in the MDF. In fact, the percentage of bamboo spp. saplings available was greater where there was more *L. camara* in all three habitats, and no bamboo spp. saplings were found in the TF where *L. camara* was absent. While this result does not indicate that this species requires *L. camara* to grow, it does appear to indicate that *L. camara* is affecting species composition by suppressing some species and facilitating the expansion of others such as bamboo spp. (A. A. Desai, pers. obs.). Such changes in the vegetation composition may have a cascading impact on the ecosystem and

would potentially impact all biodiversity. Further, we hypothesized that greater bamboo spp. sapling numbers occur within *L. camara* areas possibly because herbivores are unable to access these saplings. Other studies have shown that native plant species can benefit from invasive plant species by growing inside stands of the invasive species thereby experiencing lower levels of herbivory (Atwater *et al.* 2011). This association would allow these saplings to grow but herbivores may be feeding more on certain species where there is less *L. camara* thereby depleting their food resources in areas without *L. camara*. Although bamboo spp. are often suggested as being important elephant food plants, one estimate indicates that they made up only approximately 4.4% of elephant diet in Mudumalai (Baskaran *et al.* 2010). Therefore, our results suggest that *L. camara* presence and abundance, habitat and environmental covariates are associated with the abundance of some elephant food plants, but this association varies depending on the species and in which habitat these species are found.

#### Percentage grass cover and occupancy

The presence of *L. camara* was observed to have a significant negative association with grass cover in the MDF and DDF. The DDF was reported to have the maximum grass species richness, followed by the TF (Kumar 2011). In addition, the annual net primary productivity of grass was estimated to be highest ( $720 \text{ g m}^{-2}$ ) in the DDF,  $352 \text{ g m}^{-2}$  in the TF and  $110 \text{ g m}^{-2}$  in the MDF (Baskaran *et al.* 2010). The association of *L. camara* may not be seen in the TF due to the lower grass biomass in this habitat when compared with the MDF and DDF.

In addition, there are other factors that could potentially contribute to the absence of any association of *L. camara* in the TF. For example, cattle grazing has been regarded as one of the causes of the depletion of grass in the thorn forest, and the TF has been considered as sub-optimal habitat for elephant due to low productivity of grass (Daniel *et al.* 1995) allowing *L. camara* to invade these sites (Silori & Mishra 2001) yet not have a significant association with grass cover in the TF.

From our observations within the reserve, the most visible association of *L. camara* on elephant habitat appeared to be the loss of grass cover. Our analysis indicated a significant negative association between percentage grass occupancy and *L. camara*. This result possibly indicates competition for the same space, nutrients or water. A previous study in Mudumalai indicated that in the dry deciduous forest, 85% of elephant diet was grass, while 78% and 53% of elephant diet consisted of grass in the MDF and TF respectively

(Baskaran *et al.* 2010). The reduction in grass cover could lead to food limitation for elephant and other herbivores that depend on grass in the reserve. Reduced grass cover could lead to a reduced carrying capacity of herbivores in the reserve. Any adverse impact on herbivores that are dependent on grass would in turn impact large carnivores such as tigers which are dependent on them (Prasad 2010).

Overall the replacement of grass by *L. camara* could have serious conservation implications for both herbivores and their predators. Unpalatable weeds such as *L. camara* may render some areas unsuitable to elephant through reduced forage, limiting food to fewer patches. Such changes in carrying capacity and distribution of food resources of the reserve could also result in elephants being forced to move out in search of better forage. This movement would likely occur with high elephant densities, if food becomes more limiting. Managers in particular need to recognize that reduced carrying capacity through loss of grazing areas can force elephants to move out of the reserve and come into increased conflict with the surrounding human settlement (Ishwaran 1993). It is important that managers take this into account and address this situation. For example, seeds of grass species such as *Axonopus* sp. that compete well with *L. camara* could be sowed to help increase forage for grazers (Kumar *et al.* 2012).

#### Conclusions

The results of our study indicate that *L. camara* appears capable of altering plant species assemblage, some elephant browse plants and percentage grass cover in the MDF and DDF in addition to other factors. It appears that *L. camara* invasion is not associated with plant species assemblage, elephant browse plants and grass cover in the TF despite the thorn forest having the highest number of invaded sites. These results suggest that *L. camara* may not be responsible for any changes brought about to the plant community within the TF. This lack of association also suggests that managers may instead focus on *L. camara* management in the MDF and DDF of Mudumalai where *L. camara* does have a significant association with the plant community. Nevertheless, as in many invaded systems, there is still uncertainty as to whether *L. camara* is the 'driver' of community changes or is just a 'passenger' that appears to be less affected by disturbance or environmental stressors and may just be an opportunistic invader (MacDougall & Turkington 2005). Further studies are required to empirically test whether *L. camara* is the 'driver' of plant community changes or just a 'passenger' that is a consequence of a disturbed habitat.

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**Appendix 1.** The list of plant species (shrubs and saplings measuring between 10 and 150-cm in height) identified in the plots along the 67 1-km in length transects in Mudumalai Tiger Reserve, India. Number refers to the total number of individual stems of the species counted throughout the reserve.

Plant species	Number
<i>Acacia leucophloea</i> (Roxb.) Willd.	13
<i>Acacia</i> spp.	22
<i>Achyranthes aspera</i> L.	3
<i>Actinodaphne malabarica</i> Balkr.	12
<i>Albizia lebbek</i> (L.) Benth.	16
<i>Allophylus cobbe</i> (L.) Raeusch.	5
<i>Anisochilus scaber</i> Benth.	7
<i>Anogeissus latifolia</i> (DC.) Wallich ex Guill. & Perr.	62
<i>Antidesma menasu</i> (Tul.) Miq. ex Muell.-Arg.	7
<i>Ardisia solanacea</i> Roxb.	8
<i>Argeratum conyzoides</i> L.	9
<i>Argyrea cuneata</i> (Willd.) Ker Gawler	10
<i>Azadirachta indica</i> Adr. Juss.	1
<i>Bambusa arundinacea</i> (Retz.) Willd.	94
<i>Bauhinia racemosa</i> Lam.	9
<i>Bidens pilosa</i> L.	6
<i>Bischofia javanica</i> Blume	7
<i>Bridelia crenulata</i> Roxb.	8
<i>Bridelia retusa</i> (L.) Spreng.	9
<i>Butea monosperma</i> (Lam.) Taubert	4
<i>Callicarpa tomentosa</i> (L.) Murr.	3
<i>Canthium dicoccum</i> (Gaertner) Teijsm. & Binnend.	30
<i>Canthium parviflora</i> Roxb.	1
<i>Capparis zeylanica</i> L.	1
<i>Careya arborea</i> Roxb.	7
<i>Carissa carandas</i> L.	2
<i>Casearia esculenta</i> Roxb.	42
<i>Cassia fistula</i> L.	132
<i>Cassia sophora</i> L.	4
<i>Cassia tora</i> L.	17
<i>Catunaregum spinosa</i> (Thunb.) Tirveng.	340
<i>Celosia argentea</i> L.	4
<i>Celtis tetrandra</i> Roxb.	1
<i>Chloroxylon swietenia</i> DC.	5
<i>Cinnamomum malabathrum</i> (Lam.) J.Presl	23
<i>Cinnamomum</i> spp.	3
<i>Cipadessa baccifera</i> (Roth) Miq.	25
<i>Coffea robusta</i> L.	23
<i>Cordia wallichii</i> Don.	33
<i>Dalbergia lanceolaria</i> L.f.	42
<i>Dalbergia latifolia</i> Roxb.	69
<i>Desmodium pulchellum</i> (L.) Benth.	43
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	8
<i>Diospyros montana</i> Roxb.	83
<i>Elaeodendron glaucum</i> (Rottb.) Pers.	1
<i>Eriolaena hookeriana</i> Wight & Arn.	5
<i>Eriolaena quinquelocularis</i> Wright	3
<i>Erythrina indica</i> Lam.	2
<i>Erythroxylum monogynum</i> Roxb.	11
<i>Euphorbia hirta</i> L.	7

## Appendix 1. Continued.

Plant species	Number
<i>Ficus religiosa</i> L.	2
<i>Flacourtia indica</i> (Burm.f.) Merr.	3
<i>Flueggea leucopyrus</i> Willd.	13
<i>Gardenia gummifera</i> L.f.	2
<i>Garuga pinnata</i> Roxb.	6
<i>Givotia rottleriformis</i> Griffith	1
<i>Glochidion zeylanicum</i> (Gaertn.) A.Juss.	5
<i>Glycosmis pentaphylla</i> (Retz.) DC.	67
<i>Gmelina arborea</i> Roxb.	8
<i>Grewia hirsuta</i> Vahl	58
<i>Grewia orbiculata</i> Wall.	2
<i>Grewia tiliifolia</i> Vahl	156
<i>Haldina cordifolia</i> (Roxb.) Ridsd.	3
<i>Hardwickia binata</i> Roxb.	1
<i>Helicteres isora</i> L.	45
<i>Ipomoea hederifolia</i> L.	6
<i>Kydia calycina</i> Roxb.	88
<i>Lagerstroemia microcarpa</i> Wight	21
<i>Lagerstroemia parviflora</i> Roxb.	5
<i>Lansea coromandelica</i> (Houtt.) Merr.	4
<i>Lawsonia inermis</i> L.	1
<i>Litsea floribunda</i> Gamble	3
<i>Litsea mysorensis</i> Gamble	10
<i>Madhuca indica</i> J. Gmelin	2
<i>Maesa indica</i> (Roxb.) A.DC.	4
<i>Mallotus philippensis</i> (Lam.) Muell. Arg.	6
<i>Mangifera indica</i> L.	4
<i>Maytenus emarginata</i> (Willd.) Ding Hou	13
<i>Melia dubia</i> Cav.	4
<i>Mitragyna parviflora</i> (Roxb.) Korth.	2
<i>Murraya paniculata</i> (L.) Jack	19
<i>Naringi crenulata</i> (Roxb.) Nicolson	12
<i>Nothapodytes foetida</i> (J. Graham) Mabb.	2
<i>Ocimum tenuiflorum</i> L.	1
<i>Olea dioica</i> Roxb.	45
<i>Olea glandulifera</i> Desf.	19
<i>Opuntia</i> spp.	30
<i>Ougeinia oojeinensis</i> (Roxb.) H. Ohashi	17
<i>Pavetta indica</i> L.	5
<i>Persea macrantha</i> (Nees) Kosterm.	16
<i>Phoenix loureirii</i> Kunth	7

## Appendix 1. Continued.

Plant species	Number
<i>Phyllanthus emblica</i> L.	177
<i>Pongamia pinnata</i> (L.) Pierre	3
<i>Premna tomentosa</i> Willd.	1
<i>Pterocarpus marsupium</i> Roxb.	36
<i>Radermachera xylocarpa</i> (Roxb.) Schumann	8
<i>Schleichera oleosa</i> (Lour.) Oken	50
<i>Schrebera swietenoides</i> Roxb.	7
<i>Scolopia crenata</i> Clos	12
<i>Shorea roxburghii</i> Don	81
<i>Solanum auriculatum</i>	14
<i>Solanum torvum</i> Sw.	18
<i>Sterculia guttata</i> Roxb.	8
<i>Sterculia urens</i> Roxb.	3
<i>Stereospermum personatum</i> (Hassk.) Chatterjee	4
<i>Stereospermum tetragonum</i> DC.	5
<i>Strychnos potatorum</i> L.f.	4
<i>Syzygium cumini</i> (L.) Skeels	50
<i>Tamarindus indica</i> L.	2
<i>Tamilnadia uliginosa</i> (Retz.) Tirveng. & Sastre	12
<i>Tectona grandis</i> L.f.	80
<i>Tephrosia purpurea</i> (L.) Pers.	6
<i>Terminalia chebula</i> Retz.	10
<i>Terminalia crenulata</i> Roth	27
<i>Terminalia paniculata</i> Roth	2
<i>Terminalia tomentosa</i> Wight & Arn.	22
<i>Toona ciliata</i> Roemer	4
<i>Urena lobata</i> L. ssp. <i>sinuata</i> (L.) Borssum.	11
<i>Viburnum punctatum</i> Buch.-Ham.ex D.Don	14
<i>Vitex altissima</i> L.f.	4
<i>Wendlandia thyrsoides</i> (Roem. & Schult.) Steud.	4
<i>Wrightia tinctoria</i> (Roxb.) R.Br.	7
<i>Xanthium indicum</i> J. Koenig	2
Zingiberaceae	20
<i>Ziziphus glabrata</i> Heyne ex Roth	1
<i>Ziziphus mauritiana</i> Lam.	2
<i>Ziziphus rugosa</i> Lam.	9
<i>Ziziphus xylopyrus</i> (Retz.) Willd.	25
<i>Ziziphus oenoplia</i> (L.) Miller	42
<i>Ziziphus xylopyrus</i> (Retz.) Willd.	30
<i>Ziziphus rugosa</i> Lam.	18