Lantana camara L. (Verbenaceae) invasion along streams in a heterogeneous landscape

Geetha Ramaswami[1] and Raman Sukumar[1,2,*]

[1]Centre for Ecological Sciences and [2]Divecha Centre for Climate Change, Indian Institute of Science, Bangalore 560 012, India

*Corresponding author (Email, rsuku@ces.iisc.ernet.in)

Streams are periodically disturbed due to flooding, act as edges between habitats and also facilitate the dispersal of propagules, thus being potentially more vulnerable to invasions than adjoining regions. We used a landscape-wide transect-based sampling strategy and a mixed effects modelling approach to understand the effects of distance from stream, a rainfall gradient, light availability and fire history on the distribution of the invasive shrub *Lantana camara* L.(lantana) in the tropical dry forests of Mudumalai in southern India. The area occupied by lantana thickets and lantana stem abundance were both found to be highest closest to streams across this landscape with a rainfall gradient. There was no advantage in terms of increased abundance or area occupied by lantana when it grew closer to streams in drier areas as compared to moister areas. On an average, the area covered by lantana increased with increasing annual rainfall. Areas that experienced greater number of fires during 1989–2010 had lower lantana stem abundance irrespective of distance from streams. In this landscape, total light availability did not affect lantana abundance. Understanding the spatially variable environmental factors in a heterogeneous landscape influencing the distribution of lantana would aid in making informed management decisions at this scale.

[Ramaswami G and Sukumar R 2014 *Lantana camara* L. (Verbenaceae) invasion along streams in a heterogeneous landscape. *J. Biosci.* **39** 717–726] **DOI** 10.1007/s12038-014-9465-5

1. Introduction

It has been hypothesized that the periodic occurrence of unused resources in space and time facilitates biological invasion (Davis *et al*. 2000). Such fluctuating resources in the environment, that occur due to disturbance events or due to the inherent variability in the environment, create niche opportunities for invading species, which aid in their establishment and persistence in an introduced range. Such fluctuation in resource availability has been shown to favour invasion only when there is heterogeneity in resources in space, time or both (Melbourne *et al*. 2007). At large spatial scales, environmental heterogeneity determines the presence of greater number of exotic species in a community (Davies *et al.* 2005). In this study, we assume that the presence of topographical features, environmental gradients and periodic disturbances are proxies for the spatial and temporal variability in resources such as moisture, light and nutrients, and explore the influence of these proxies on the distribution of an invasive plant.

Habitat edges are likely to be characterized by higher availability of resources, such as light, and propagules in comparison to adjoining areas. By virtue of having greater resource availability, edges may be especially prone to invasion (Catford *et al.* 2011). Indeed, invasive species richness has been found to be positively correlated with the number of edges in a landscape (Kumar *et al*. 2006). Edges occur naturally along riparian habitats and invasive species have been shown to occur here more often than adjoining habitats (Merriam 2003; Parendes and Jones 2000). Riparian ecosystems that are prone to flooding, and thus periodically influenced by processes such as sedimentation and removal of existing vegetation, are highly vulnerable to invasion by exotic species (Richardson *et al*. 2007). Rivers and streams

Keywords. Fire history; invasive plant; Mudumalai; rainfall gradient; seasonal streams; seasonally dry tropical forest

Published online: 16 July 2014

also act as channels for the effective dispersal of propagules (Parendes and Jones 2000; Thomas *et al*. 2006).

Streams are highly seasonal in seasonally dry tropical forests – habitats that remain poorly studied across the globe (Murphy and Lugo 1986; Sanchez-Azofeifa *et al*. 2005). These systems are quite different from the better studied riparian ecosystems that undergo catastrophic changes post flooding. Seasonal streams in seasonal forests of southern India, for instance, have been reported to have water flow for only a few hours to a few days following rainfall (Ruiz *et al*. 2010). Seasonal streams thus represent variation in water resource availability which varies not only in time (with season) but also in space (with topography). Because of the ephemeral nature of seasonal streams, their hydrological characterization is difficult (Ruiz *et al*. 2010) and the consequent impacts on species invasion are not understood well.

Frequent disturbances can result in patchiness of resources in space and time (Davis *et al*. 2000). One such disturbance is the occurrence of fire, which affects the availability of soil nutrients. For example, fires have been reported to volatilize nitrogen, and increase soil nitrogen limitation in fire-prone ecosystems (D'Antonio and Vitousek 1992). Thus, the fire regime of a region could indicate the nutrient status of the soil; parts of the landscape that burn more often could be poorer in nutrients lost due to volatilization than those that burn less often. The effects of fire on woody invasive plants and vice versa, however, remain unclear and largely unexplored (Mandle *et al*. 2011). Invasive species also optimally use light for growth and proliferation. Light-demanding invasive species could thus be negatively affected by the presence of other shading plants (e.g. Raizada *et al*. 2008; Totland *et al*. 2005).

Apart from the temporal fluctuation of resources, there can be spatial variation in resource availability. A rainfall gradient indicates how much water is available annually across space, and is likely to affect invasion in combination with proximity to streams and the occurrence of disturbances. Resource poor habitats have been found to favour the performance of native species over invasives (e.g. Burke and Grime 1996), although the opposite has also been observed (e.g. Funk and Vitousek 2007). More arid regions should thus be less susceptible to invasion than would moister regions. Alternately, proximity to stream-side habitats could be advantageous to invading species in arid habitats. Thus, a combination of spatial and temporal variation in moisture could facilitate invasion in otherwise unsuitable areas.

The relative importance of topography, disturbance and environmental gradients for invasive species distribution has seldom been explored in a single study. *Lantana camara* L. (lantana hereon), a woody shrub of South and central American origin, is currently acknowledged as one of the most invasive woody shrubs in the world (Richardson and Rejmánek 2011). Yet, the impact of lantana on watersheds and vice-versa remain largely unaddressed. In the following study, we explored the effects of heterogeneity of resource availability in terms of moisture (presence of seasonal streams and a rainfall gradient), disturbance (fire history) and light (shading by native tree species such as *Anogeissus latifolia* and *Terminalia tomentosa*) on the distribution of lantana. On the bases of the above-mentioned factors, the following hypotheses were formulated for lantana:

1. Seasonal streams, due to the changing flux in water with season, would be highly susceptible to invasion by lantana. Consequently, lantana stem abundance and area occupied by thickets would be greatest at stream-sides and would decrease with increasing distance from streams.
2. Lantana invasion along streams would interact with environmental gradients, such as that of rainfall. Lantana invasion was expected to be more severe near streams in arid areas than in wetter areas.
3. Lantana has been hypothesized to be cyclically benefitted by fires (Hiremath and Sundaram 2005). Owing to the high coppicing ability of lantana stems (Sharma *et al*. 2005) post fire, we predicted that higher fire frequency would be associated with greater number of lantana stems.
4. Lantana is observed to be intolerant to high shade (Sharma *et al*. 2005) and therefore, irrespective of distance from streams, lantana abundance and area covered would be lower in areas with greater canopy closure than in open areas.

2. Materials and methods

2.1 *Study site*

Mudumalai Wildlife Sanctuary and National Park (Mudumalai henceforth) is located in the southern Indian state of Tamil Nadu. A designated Tiger and Elephant Reserve, Mudumalai (321 km^2) is characterized by an average annual rainfall of between ~700 mm and 1700 mm along an east-west rainfall gradient. Consequently, the vegetation types here vary from tropical dry thorn forest in the east, through dry deciduous and moist deciduous forests in the central part to semi-evergreen vegetation in the west. Most of the rainfall in the western and central parts of Mudumalai is received during the months of June, July and August from the south-west Indian monsoon. The eastern part of the sanctuary receives most rainfall from the north-east monsoon later in the year. The elevation in the sanctuary varies from 460–1220 m asl, with a large part of the sanctuary lying at an elevation of 800–1100 m asl. Owing to the topography of the region, many seasonal streams occur throughout the sanctuary. These streams originate from or drain into two main perennial water sources – Benne Hole in the west and the Moyar river in the eastern and central part of the sanctuary (figure 1). Mudumalai experiences ground fires during the dry season although fire frequencies differ across different regions of the sanctuary.

2.2 *Study design*

Locations for laying transects were selected from a digitized map of the streams of Mudumalai in the GIS software ArcGIS (version 9.2). The coordinates of a total of sixty points on sixty streams were extracted from the map and were used for locating them in the field. The points were selected such that they were not influenced by the presence of neighbouring streams or roads. Each point was therefore at least 300 m from the next nearest stream and 100 m from the nearest road (figure 1). At each selected location, a 150 m transect was laid perpendicular to the direction of stream flow. If the points extracted from the GIS software were not conducive for laying a perpendicular transect in the field, we searched for another site nearby, on the same stream. On each transect, we laid five 10m × 10m plots, 20 m apart, such that there was a plot at 0, 30, 60, 90 and 120 m from the stream.

We used lantana stem abundance and average area covered by lantana canopy per unit area as two measures of invasion severity. Within each plot, abundance was quantified as the total number of lantana individuals. Coppices from the same root stock were also considered as a single individual. The canopy diameter of a minimum of five random stems, or if less, then all stems was noted within each plot. For the canopy of each individual plant, the distance between two farthest opposite terminal buds on branches was considered as one diameter measurement. The canopy diameter for an individual was then calculated as the average of three such measurements. Assuming a circular shape for the canopy, the minimum area occupied by lantana within each plot was calculated.

Average percent canopy openness was obtained for each plot by taking densitometer measurements at the four corners and the centre of each plot and then averaging these values. A densiometer is an instrument with a convex mirror divided into a grid of 24 squares. Four dots were imagined within each edge of each square and the number of dots over which the overhead canopy reflected was counted. Canopy measurements were taken from four different directions. The average number of dots covered by canopy was calculated and later converted to a percentage of total number of dots. This percentage was considered as a measure for canopy closure at a point. This study was conducted over a period of eight months, from September 2009 to April 2010. It must be noted that the duration of this study overlapped with the dry season associated with the deciduous phase of trees. However, it is well documented that the deciduous phase of trees is shorter than the dry season of seasonal forests (Singh and Kushwaha 2005). We did not capture the complete deciduous phase of vegetation in any transect and therefore canopy measurements taken during the dry season (December 2009 – April 2010) were comparable to those from the relatively wetter months (September – November 2009).

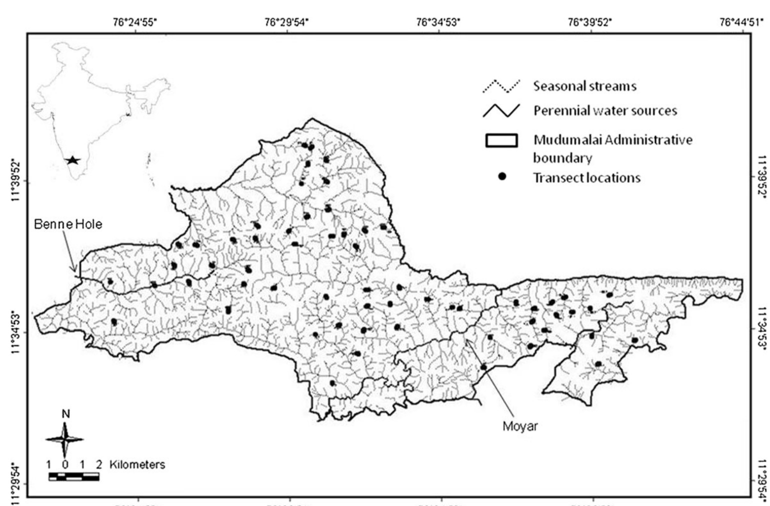

Figure 1. Mudumalai Wildlife Sanctuary and National Park, located in the southern Indian state of Tamil Nadu (inset). The map shows the location of perennial and seasonal water sources within the sanctuary. Transects were laid at selected sites and lantana invasion was measured here.

The total annual rainfall at all sampling plots were laid was extracted from rainfall maps for the reserve. The rainfall map was constructed using data from 13 rain gauges located in and around the sanctuary. Data from the years 1990 to 2007 were used to generate an interpolated surface map of rainfall using the kriging method. The fire history, in terms of the amount of area burnt annually, is known for the sanctuary from 1989 to the present. The frequency of fire occurrence is also known at the scale of each 100m × 100m for the entire sanctuary. We extracted the total number of fires that have occurred at all plots within the sixty transects from a fire frequency map for the duration from 1989 to 2010. The spatial locations of some plots within a few transects (usually the second and the fourth) were not recorded. In such a situation, the average of the fire frequency and rainfall for these plots were obtained by averaging extracted values for the two nearest plots on either side.

2.3 *Statistical analyses*

We used a linear mixed effects approach to model the abundance and area covered by lantana to account for possible spatial autocorrelation between plots within a given transect. We specified separate models for lantana abundance and area covered by lantana stems, henceforth referred to as the abundance model and the area model respectively. Distance from stream (0, 30, 60, 90, 120 m), annual rainfall, fire frequency and average openness of a plot were specified as fixed effects while Transect ID was taken as the random effect. In order to test hypothesis 2, an interaction term between distance from streams and annual rainfall was also considered. Since lantana stem abundance was a count and lantana area was log-normally distributed, we used a log transformation +1 on both response variables. Outliers were identified by visual examination of patterns in the raw data and were excluded from the analyses. The function lmer (package lme4)(Bates *et al*. 2011) was used to create models in the statistical programming software R, version 2.13.1 (R Core Development Team 2011). We used graphical diagnostics recommended in order to test for assumptions of normality, independence and homogeneity of model residuals (Zuur *et al*. 2009). We simplified models by sequentially dropping terms and assessed the significance of model terms on the basis of the likelihood ratio test (LRT) after fitting the mixed effects model with the maximum likelihood (ML) method instead of the default restricted maximum likelihood (REML) method(Zuur *et al*. 2009). We specified orthogonal tests (Helmert contrasts) in the minimum adequate model to compare mean lantana abundance and area covered at different distances from the stream. The use of orthogonal contrasts overcomes the issue of multiple comparisons and corrections for the same are thus not required. The Helmert contrasts compare the following groups of means with respect to distance from streams – overall mean with the mean of 30–120 m, mean of 30–60 m with that of 90–120 m, mean at 90 m with that of 120 m and finally mean of 30 m with that of 60 m. The parameter estimates that appear in the summary of such a model are thus differences between the above mentioned means. The models were refitted with the REML criterion before computing the highest posterior densities for parameters obtained from 10,000 Markov chain Monte Carlo samples (using the functions mcmcsamp and HPDinterval in R). 95% confidence intervals (henceforth CI) on differences between group means were obtained thus. Parameters with 95% CIs that did not overlap with zero were considered as being statistically significant.

3. Results

3.1 *General patterns*

Lantana was present in 72% of all plots sampled with 26% of the plots having more than 10 stems each. The number of stems recorded in a given plot ranged from 0 to 79. Lantana cover in plots ranged from 0 to 100 m^2, the latter occurring when the entire plot was covered with lantana. Lantana stem abundance decreased with increasing distance from streams, although these estimates were extremely variable (table 1). Although area covered by lantana was lower at 120 m than at 0 m, there was a slight increase observed between 30 to 90 m (figure 2). The number of lantana stems and area was highly

Table 1. Observed variability in the abundance and area covered by lantana stems per 100 m^2 across sampled transects with respect to the explanatory factors examined

Factors	Lantana abundance (stems/100 m^2)	Lantana area (m^2/100 m^2)
Distance from stream (m)		
min (0 m)	10 .1 (6.2)	21.3 (4.3)
max (120 m)	6.8 (5.1)	13.3 (2.5)
Annual rainfall (mm)		
low (800–1100 mm)	11.6 (6.7)	12.3 (1.3)
medium (1100–1300 mm)	5.2 (4.4)	16.9 (2.2)
high (1300–1600 mm)	7.6 (5.4)	26.4 (3.7)
Fire frequency		
low (0 events)	24.3 (9.6)	11.9 (6.7)
high (11 events)	3.5 (3.6)	1.3 (0.57)
Percent open		
low (0–40%)	7.2 (5.3)	16.8 (1.3)
medium (40–70%)	9.7 (6.1)	13.3 (3.3)
high (70–100%)	5.5 (4.6)	8.9 (1.1)

Numbers in parentheses indicate ± SE.

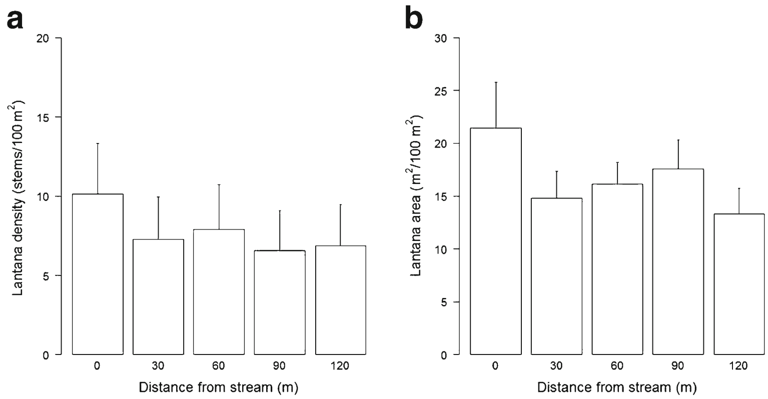

Figure 2. Effect of distance from streams on mean lantana stem abundance (**a**) and mean area occupied per plot (**b**). Error bars represent + SE. Number of lantana stems and area occupied by lantana decreased with increasing distance from streams.

variable across the rainfall gradient. While the number of lantana stems decreased marginally from areas with low (800–1100 mm) annual rainfall to areas with high (1300–1600 mm) rainfall, the number was lowest in areas with medium annual rainfall (table 1). Area occupied by lantana was highest in high rainfall areas, followed by medium and low rainfall areas. Plots that had burnt only once between 1989 and 2010 supported many more lantana stems and larger lantana area than plots that had burnt a maximum of 11 times (table 1). Lantana attributes also varied considerably with percent openness of the canopy. Lantana was more abundant under medium shade (40–70% open) than in high (0–40% open) or low shade (70–100% open; table 1). Area occupied by lantana was highest in the least open plots and decreased in plots that were most open (table 1).

3.2 *Model outputs*

Variation in lantana stem abundance was explained by distance from stream (LR statistic = 24.88, $P \ll 0.001$) and fire history (LR statistic = 35.08, $P \ll 0.001$). Variation in area covered by lantana was explained by distance from stream (LR statistic = 12.3, $P = 0.015$), fire history (LR statistic = 30.28, $P \ll 0.001$) as well as the rainfall gradient (LR statistic = 6.45, $P = 0.011$). However, the coefficient for the rate of increase of lantana area with increasing rainfall at constant fire frequency was relatively small (Table 2). Percent shade as well as the interaction between annual rainfall and distance from stream dropped out of the minimum adequate models as being insignificant. Both models showed high predictive power (Spearman's correlation test between observed and predicted response, R (abundance model) = 0.86, R (area model) = 0.73). Within transect variation of lantana response was 0.45 for the lantana abundance model and 0.25 for the area model. Stem abundance and area covered was highest immediately adjacent to stream (i.e. at 0 m) and significantly greater than the abundance at all other distances from the stream (table 2; figure 2). Lantana stem abundance decreased with increasing number of fires (figure 3). When fire frequency was kept constant at a value of 2 (a value that occurred across the rainfall gradient), area covered by lantana was predicted to increase with increasing annual rainfall (figure 4).

4. Discussion

Our study explored the effects of heterogeneity in spatial moisture availability, disturbance history and local conditions such as light availability on the stem abundance and area occupied by the invasive shrub lantana. Our results indicate that lantana possibly utilizes streams and stream-side habitats for persisting in and spreading over a heterogeneous landscape.

Although this study was designed to chiefly detect the effects of streams on the severity of lantana invasion, the multiple-variable mixed effects model allowed us to detect the effects of other co-occurring variables as well. Higher light availability at ground level was expected to increase the severity of lantana invasion. The percentage cover and relative growth rate of lantana decrease with increasing distance from the centre of a gap and larger gaps support larger individuals (Raizada *et al*. 2008, Totland *et al*. 2005). Lantana abundance has also been found to decrease with increasing tree density at the landscape scale (Prasad 2011). We found that relative openness of a plot did not affect lantana. One reason for this could be that very high or very low shade was rarely encountered and that, on average, plots

Table 2. Outputs of the mixed-effects models for lantana abundance and area covered by lantana along streams

	Estimate	SE	t value	95% CI (lower)	95% CI (upper)	
Abundance model						
Fire history	−0.197	0.029	−6.861	−0.244	−0.159	*
Distance from stream						
Grand mean	2.652	0.190	13.964	2.396	2.956	*
Grand mean vs 30–120 m	0.096	0.019	4.972	0.054	0.140	*
30–60 m vs 90–120 m	0.088	0.043	2.037	−0.004	0.187	ns
90 m vs 120 m	0.010	0.062	0.164	−0.122	0.150	ns
30 m vs 60 m	−0.051	0.061	−0.839	−0.177	0.088	ns
Area model						
Fire history	−0.184	0.031	−5.933	−0.234	−0.130	*
Rainfall	0.002	0.001	3.382	0.001	0.003	*
Distance from stream						
Grand mean	1.050	0.585	1.794	0.094	1.968	*
Grand mean vs 30–120 m	0.080	0.028	2.866	0.016	0.136	*
30–60 m vs 90–120 m	0.097	0.068	1.438	−0.047	0.240	ns
90 m vs 120 m	0.185	0.101	1.835	−0.006	0.417	ns
30 m vs 60 m	−0.084	0.091	−0.925	−0.294	0.097	ns

'*' denotes a difference in means that is significantly greater than zero; the 'estimate' for a given parameter is the slope for the rate of change in lantana stem abundance and area for a continuous variable (Fire history, Rainfall) or the comparison of means (as described in the Methods section) for distance from stream.

were 26% open. Interaction between light and other independent variables that could affect the performance of lantana could also not be detected in this study.

We expected lantana to show greater abundance and cover more area in regions of Mudumalai that experienced higher fire frequency, but found the opposite. An earlier study from the neighbouring dry deciduous forest reserve of Bandipur Tiger Reserve showed that fire history over a short time span (7 years) did not influence lantana biomass (Prasad 2011). Invasive plants are known to interact with fire often altering regimes in a positive feedback loop. For instance, some invasive grass species have been shown to cyclically facilitate the occurrence of fire and benefit from such events (D'Antonio and Vitousek 1992). The cyclic propagation of fire has been hypothesized as a mechanism even for lantana invasion (Hiremath and Sundaram 2005). By rapidly building up biomass that readily burns during the dry season and coppicing profusely during the wet season, creating more biomass for burning, lantana could maintain a fire cycle that is different from current fire regimes. Since this study was conducted largely in the dry season, the abundance and area occupied in frequent-fire areas is possibly underestimated and a similar study needs to be undertaken in the wet season in order to determine whether frequent fires indeed suppress lantana. Furthermore, the fire frequency is highest in the north-central part of Mudumalai (Kodandapani *et al*. 2004), which is characterized by stunted growth forests dominated by a dipterocarp (*Shorea roxburghii*) and shallow soils that seem different from the rest of Mudumalai. The combination of edaphic factors, vegetation type and prevalent disturbances need to be explored in more detail in order to tease apart their individual effects on lantana distribution.

The interaction term between rainfall and distance from stream was not significant. Thus, there seemed to be no greater advantage for lantana to be along streams in drier areas than in moister areas of this landscape. This could be due to the functional strategies that lantana uses to persist. Lantana has been reported to have drought avoidance strategies such as a deep root system and greater water retention than a native congener in the Galapagos islands, allowing it to proliferate even in very arid regions (Castillo *et al*. 2007). The rainfall gradient by itself, however, influenced the area covered by lantana – wetter regions of the landscape harboured larger lantana canopies. It must be noted that the gradient of rainfall across Mudumalai falls well within the range of reported tolerance of lantana (700–3000 mm annual rainfall, Swabrick *et al.* 1998), indicating that lantana can thrive equally well at the two extremes of rainfall in this landscape. The exact mechanism by which lantana gains competitive advantage over native species along the rainfall gradient cannot be discerned from this study. When fire frequency was kept constant at low values, the area occupied by lantana increased with increasing rainfall. This could

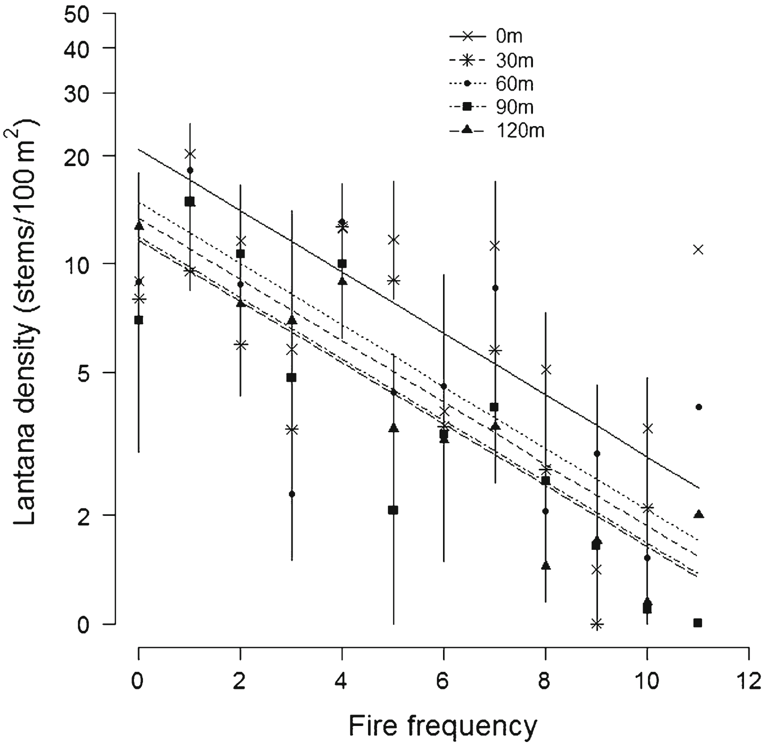

Figure 3. Effects of fire frequency on the number of lantana stems. Lines indicate predictions form the mixed-effects models, points indicate observed data and error bars on the points indicate ± SE. Lantana stem abundance per plot decreased with increasing fire frequency (number of fire occurrences between 1989 and 2010), irrespective of distance from streams. Note that the y axis has been modified to represent lantana abundance in the transformed logarithmic scale.

simply be an artefact of the spatial distribution of fire occurrence in Mudumalai. The regions with low fire frequency, confined to the western and eastern extremities of Mudumalai that experience the highest and lowest annual rainfall, respectively, are also regions with relatively lower densities of lantana (G Ramaswami, pers. obs.).

Invasion by terrestrial plants along stream corridors is often related to overbank flooding (Thomas *et al*. 2006). Although seasonal streams in dry forests such as the ones sampled in Mudumalai do not experience dramatic flooding, we nevertheless observed higher densities of lantana closest to the streams. The stream-utilization pattern may reflect the physiological capability of lantana to utilize moisture efficiently rather than benefitting from resource spurts occurring as a result of flooding. Although not reported in lantana, species such as *Alliaria petiolata* are known to perform better in soils with high moisture content (Meekins and McCarthy 2001). Streams also carry propagules of invasive species to new sites, allowing invasive species to colonize areas along stream corridors. This phenomenon has been observed in *Dioscorea oppositifolia* (Thomas *et al*. 2006), wherein vegetative bulbils dispersed through streams colonize stream-sides. Similarly, seasonal streams probably facilitate the arrival of lantana seeds at stream-sides as well, although this process is not reported in literature. Lantana fruits profusely (Babu *et al.* 2009) and the large number of seeds produced along stream sides very likely cause secondary infestations down-stream, if indeed propagules disperse via seasonal streams. Another possible reason for observing greater invasion severity at stream-sides is that once established, invasive plants alter site conditions such that they favour the persistence of invasive populations over native populations. For example, plants such as *Tamarix* and *Acacia* spp. that invade riparian habitats in arid regions, apart from altering native vegetation composition, also alter the hydrological properties of the river, such as reducing stream flow (Galatowitsch and Richardson 2005). The impacts of lantana on the hydrology of seasonal streams and the consequent impacts on native species diversity and performance are currently unknown. It is necessary that such studies be undertaken immediately and that appropriate management action be devised accordingly.

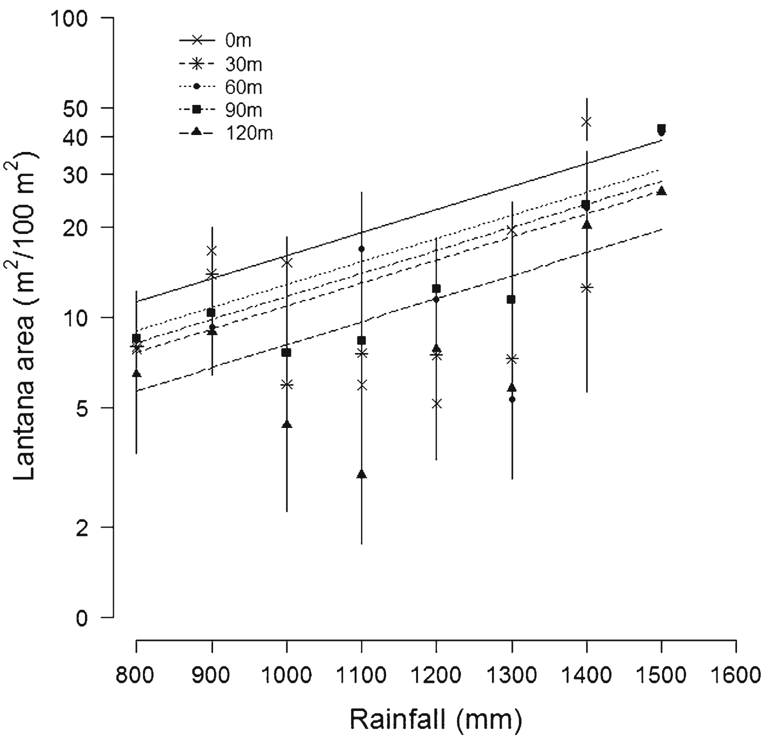

Figure 4. Effect of a rainfall gradient on the area occupied by lantana, when fire frequency is held constant at a value of 2. Lines indicate predictions form the mixed-effects models, points indicate observed data and error bars indicate ± SE. Lantana area seems to increase with increasing rainfall, irrespective of distance from streams. Note that the y axis has been modified to represent lantana area in the transformed logarithmic scale.

The presence of seasonal streams, rainfall gradients and fire history influence the distribution of the woody invasive shrub *Lantana camara*. We speculate that lantana utilizes spatially clumped resources such as moisture near streams efficiently, and thus persists and spreads even in arid regions. Native diversity especially in protected areas has been shown to be adversely affected by the presence of lantana (Prasad 2010, Sundaram and Hiremath 2012), although in another study we have found the effects of lantana to be largely neutral on woody native species (Ramaswami and Sukumar 2011). However, habitat and forage quality in such dry forests may be affected by the presence of lantana, in turn affecting the herbivore community and eventually the large carnivores dependent upon this prey base (Prasad 2010). The suite of management practices that have been followed for the past century or so across continents have been largely ineffective in curtailing the spread of lantana (Bhagwat *et al*. 2012) and it is imperative that we acquire a deeper understanding of its ecology before devising control measures. Understanding the spatially variable factors that influence distribution of lantana would aid managers to identify high-risk zones that should be monitored intensively and receive targeted management. We conclude that a heterogeneous landscape offers a multitude of niche opportunities to an invader and that this heterogeneity should be a key consideration in devising invasive plant management actions.

Acknowledgements

We thank the Forest Department of Tamil Nadu state for granting us permission to conduct this study and the Ministry of Environment and Forests, India, for funding this study. We thank field assistants M Bomman, Kunmari, Alan and Bantan for help with data collection. Rainfall maps were generated by Sandeep Pulla and Nandita Mondal. All rainfall data and fire data from

1989–2004 were collected by CM Bharanaiah, HS Dattaraja and HS Suresh. Fire data post 2004 was collected and collated into a landscape-wide fire frequency map by Nandita Mondal.

References

Bates D, Maechler M and Bolker B 2011 Linear mixed-effects models using S4 classes. R package version 0.9975–10

Babu S, Love A and Babu CR 2009 Ecological restoration of Lantana-invaded landscapes in Corbett Tiger Reserve, India. *Ecol. Restor.* **27** 467–477

Bhagwat SA, Breman E, Thekaekara T, Thornton TF and Willis KJ 2012 A battle lost? Report on two centuries of invasion and management of *Lantana camara* L. in Australia, India and South Africa. *PLoS ONE* **7** e32407

Burke MJW and Grime JP 1996 An experimental study of plant community invisibility. *Ecology* **77** 776–790

Castillo JM, Leira-Doce P, Carrión-Tacuri J, Muñoz-Guacho E, Arroyo-Solís A, Curado G, Doblas D, Rubio-Casal AE, *et al.* 2007 Contrasting strategies to cope with drought by invasive and endemic species of Lantana in Galapagos. *Biodivers. Conserv.* **16** 2123–2136

Catford JA, Vesk PA, White MD and Wintle BA 2011 Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. *Divers. Distrib.* **17** 1099–1110

D'Antonio CM and Vitousek PM 1992 Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* **23** 63–87

Davies KF, Chesson P, Harrison S, Inouye BT, Melbourne BA and Rice KJ 2005 Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* **86** 1602–1610

Davis MA, Grime JP and Thompson K 2000 Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88** 528–534

Funk JL and Vitousek PM 2007 Resource-use efficiency and plant invasion in low-resource systems. *Nature* **446** 1079–1081

Galatowitsch S and Richardson DM 2005 Riparian scrub recovery after clearing of invasive alien trees in headwater streams of the Western Cape, South Africa. *Biol. Conserv.* **122** 509–521

Hiremath A and Sundaram B 2005 The fire-lantana cycle hypothesis in Indian forests. *Conserv. Soc.* **3** 26–42

Kodandapani N, Cochrane MA and Sukumar R 2004 Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conserv. Biol.* **18** 1553–1561

Kumar S, Stohlgren TJ and Chong GW 2006 Spatial heterogeneity influences native and non-native species richness. *Ecology* **87** 3186–3199

Mandle L, Bufford JL, Schmidt IB and Daehler CC 2011 Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. *Biol. Invasions* **13** 1815–1827

Meekins JF and McCarthy BC 2001 Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecol. Appl.* **11** 1336–1348

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, Harrison S, *et al.* 2007 Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecol. Lett.* **10** 77–94

Merriam RW 2003 The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. *J. Torrey Bot. Soc.* **130** 283–291

Murphy PG and Lugo AE 1986 Ecology of dry tropical forest. *Ann. Rev. Ecol. Syst.* **17** 67–88

Parendes LA and Jones JA 2000 Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conserv. Biol.* **14** 64–75

Prasad AE 2010 Effects of an exotic plant invasion on native understory plants in a tropical dry forest. *Conserv. Biol.* **24** 747–757

Prasad AE 2011 Landscape-scale relationships between the exotic invasive shrub *Lantana camara* and native plants in a tropical deciduous forest in southern India. *J. Trop. Ecol.* **28** 55–64

R Core Development Team 2011 *R: A language and environment for statistical computing.* (R Foundation for Statistical Computing) <http://www.R-project.org.>

Raizada P, Sharma GP and Raghubanshi AS 2008 Ingress of lantana in dry tropical forest fragments: Edge and shade effects. *Curr. Sci.* **94** 180–182

Ramaswami G and Sukumar R 2011 Woody plant seedling distribution under invasive *Lantana camara* thickets in a dry-forest plot in Mudumalai, southern India. *J. Trop. Ecol.* **27** 365–373

Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P and Hobbs RJ 2007 Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Divers. Distrib.* **13** 126–139

Richardson DM and Rejmánek M 2011 Trees and shrubs as invasive alien species – a global review. *Divers. Distrib.* **17** 788–809

Ruiz L, Varma MR, Kumar MM, Sekhar M, Marechal JC, Descloitres M, Riotte J, Kumar S, *et al.* 2010 Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. *J. Hydrol.* **380** 460–472

Sanchez-Azofeifa G, Quesada M, Rodriguez J, Nassar J, Stoner K, Castillo A, Garvin T, Zent E, *et al.* 2005 Research priorities for neotropical dry forests. *Biotropica* **37** 477–485

Sharma GP, Raghubanshi AS and Singh JS 2005 Lantana invasion: An overview. *Weed Biol. Manage.* **5** 157–165

Singh KP and Kushwaha CP 2005 Emerging paradigms of tree phenology in dry tropics. *Curr. Sci.* **89** 964–975

Sundaram B and Hiremath A 2012 *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation. *Biol. Invasions* **14** 1127–1141

Swabrick JT, Wilson BW and Hannan-Jones MA 1998 *Lantana camara* L; in *The Biology of Australian Weeds* (eds) FD Panetta, RH Groves and RCH Shepherd (Melbourne: RG and FJ Richardson) pp 119–136

Thomas RJ, Middleton B and Gibson DJ 2006 A landscape perspective of the stream corridor invasion and habitat characteristics of an exotic (*Dioscorea oppositifolia*) in a pristine watershed in Illinois. *Biol. Invasions* **8** 1103–1113

Totland O, Nyeko P, Bjerknes A, Hegland SJ and Nielsen A 2005 Does forest gap size affects population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? *Forest Ecol. Manag.* **215** 329–338

Zuur AF, Leno EN, Walker NJ, Saveliev AA and Smith GM 2009 *Mixed effects models and extensions in ecology with R*. (Springer Science + Business Media)

MS received 03 September 2013; accepted 30 June 2014

Corresponding editor: R Geeta