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IMPACT OF THE INVASIVE WEED *LANTANA CAMARA* (VERBENACEAE) ON BUTTERFLY BEHAVIOUR AND HABITAT USE IN A TROPICAL FOREST IN INDIA.

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ABSTRACT. Invasive species are thought to influence native biodiversity through a wide range of direct and indirect effects. We examined the influence of an invasive plant, *Lantana camara*, on butterfly assemblages in a tropical forest in India. *Lantana camara* typically dominates the understorey in invaded areas and might therefore reduce the availability of resources and microhabitats essential for butterflies. We hypothesized that butterflies would show reduced use of lantana-dominated habitat when compared with native vegetation. We evaluated such reduced habitat use by testing for (1) reduced levels of behaviours other than feeding and (2) fewer butterfly species and individuals in lantana-dominated habitat patches. To test these expectations, three plots of 30 × 30 meters each were laid in lantana-dominated and native-vegetation patches. In total, three plots in native-vegetation and three in lantana-dominated habitat were marked. Butterfly behaviour was measured through focal-animal follows, and abundance and species numbers were investigated using point sampling inside these plots. We found that butterflies showed substantial behavioural differences between lantana-dominated and native-vegetation plots, indicating a possiblity that the invaded patches were relatively less suitable for several butterfly activities. Furthermore, fewer butterfly species and individuals were seen in lantana-dominated compared with native-vegetation habitat, indicating that lantana invasion results in reduced suitability of a habitat. Whether local behavioural effects of invasive plants, such as reduced habitat use, can lead ultimately to reduced population sizes and local extinctions will need to be examined.

Additional key words: Invasive species, butterflies, tropics.

Invasive alien species are considered to be a major threat to native biodiversity (Calvero and García-Berthou 2005). One such invasive plant species, *Lantana camara* (henceforth lantana), was introduced into India in the 1800s as an ornamental plant (Kohli et al. 2006), and is amongst the most widespread terrestrial invasive species in India today (Love et al. 2009). Lantana is also one of the hundred most invasive species globally (Lowe et al. 2000). Despite its importance, the effect of lantana on native faunal diversity is poorly understood. Existing studies focus on patterns in the spread of lantana (e.g., Sundaram and Hiremath 2012); and its effect on native plants (e.g., Gooden et al. 2009, Ramaswami and Sukumar 2011, Sharma and Raghubanshi 2007) and ecosystem properties, such as propensity to fire (Hiremath and Sundaram 2005). Indeed, more generally, relatively little is known about the potential impacts of invasive plants on higher trophic levels (see Gerber et al. 2008).

We studied the impact of lantana on butterflies, an important set of floral pollinators (Radar et al. 2015). While there is some information on how invasive plants may influence temperate butterfly assemblages (e.g., Moron et al. 2009, Preston et al. 2012), very little is known regarding the effects of invasive plants on tropical butterflies (Bonebrake et al. 2010). The effect of lantana on butterflies is likely to be complex. As lantana flowers abundantly and, in many parts of India, almost throughout the year, the nectar resources provided by lantana may benefit butterfly species able to make use of this resource. Several relatively large butterfly species feed on lantana nectar (Boggs et al.1981, Schemske 1976, Kunte 2008). However, lantana does not provide other resources needed by butterflies. For example, to our knowledge, there is no evidence in the literature for the use of lantana by native butterflies as larval host plants. The lack of suitable resources, other than nectar (adult forage), may be further exacerbated by the typical pattern of lantana spread in a habitat. Lantana displaces native vegetation in the understorey and heavily infests areas, thereby reducing native-vegetation abundance and diversity in an area (Sharma et al. 2005). Since most of the larval host-plants of the butterflies are native plant species this reduction could negatively influence butterflies by reducing the abundance and diversity in resources and microhabitats required by butterflies: butterflies require a complex mixture of nectar plants, larval host plants, puddling areas, basking and resting places (Sharp and Parks 1974), and butterfly diversity is thought to correlate positively with habitat heterogeneity (Tews et al. 2004).

We examined the influence of heavy lantana infestation on butterfly behaviour and habitat use in a tropical forest in India. As described previously, while lantana-dominated habitat may provide nectar resources for adults, they may not be as rich in other required resources, such as larval host plants. We therefore hypothesized that butterflies show reduced use of lantana-dominated habitat when compared with native vegetation. Two ways in which reduced habitat use by butterflies may manifest itself are (1) through reduced levels of behaviours (basking, flying, resting and territorial chases) other than feeding behaviour (since lantana is a rich nectar source) in lantana-dominated habitat compared with native vegetation; and (2) through fewer butterfly species and individuals occurring in lantana-dominated habitat. To test these predictions, we compared butterfly behaviour and the number of different butterfly species seen using a forest site. We also compared butterfly abundance in habitat dominated by lantana with those in native vegetation habitats.

Methods

Study Sites

The study was carried out in Biligiri Rangaswamy Temple Tiger Reserve (77º–77º66' E, and 11º 47'–12º 09' N), hereafter 'BRT', located in Chamarajanagar district in the Indian state of Karnataka. The sanctuary, 540 km^2 in area, is composed of small hills and valleys. Dry-deciduous and moist-deciduous forest cover most parts of the sanctuary, with scrub forest at lower elevations around the periphery of the sanctuary, patches of riparian, semi-evergreen, evergreen and shola forests on the hill tops. Lantana has invaded throughout the study area extensively including forest gaps, road edges and also the understorey in all forest types (Sundaram and Hiremath 2012).

Study plots were laid in moist-deciduous (MDF) and semi-evergreen (SEF) forest types as these generally have high lantana density (Krishnaswamy et al. 2004, Sundaram and Hiremath 2012) and also cover a large area in BRT. Within each forest type, two kinds of habitats were identified: (i) native vegetation with little (< 1% in 30 × 30 m) or no lantana in the undergrowth and (ii) vegetation dominated by lantana in the undergrowth. In these two habitats, plots measuring 30 × 30 m were marked using measuring tapes and coloured tags. In total, three plots in native-vegetation (two SEF and one MDF) and three in lantana-dominated (one SEF and two MDF) habitat were marked (Table 1). Both native-vegetation and lantana-dominated plots had similar tree abundance and primarily differed in the understorey composition (Tables 1 and 2). Two colour morphs of lantana were present in the study plots: one with pink and yellow flowers and the other with orange flowers, and the plants were around 1.5–2 meters tall. The study was conducted from February (late winter) to April (summer) in 2011 and 2012. At this study site, butterfly activity and abundance are high during two seasons – February–March and October-November (post-monsoon). Our study covered the Feb–March peak butterfly activity, but the post-monsoon season could not be studied because the study area experiences extended monsoons and retreating monsoons, which makes it difficult to study butterfly behaviour.

Behavioural observations

Observations were carried out from 0900–1700 hrs. In each plot, focal-animal sampling was combined with instantaneous sampling and all-occurrences sampling (Altmann 1974) to quantify butterfly behaviour. Each sampling session at a plot lasted one-two hours during which the plot was walked thoroughly and individuals were chosen for focal-animal follows. Only one individual per species was sampled during a sampling session to avoid sampling the same individual twice.

Nineteen butterfly species, which were relatively common, well-distributed across the study area, and seen throughout the year, were chosen as target species to study butterfly behaviour (Kunte et al. 2013). These were *Ariadne ariadne*, *Danaus genutia*, *Hypolimnas bolina*, *Hypolimnas misippus, Junonia hierta, Junonia iphita, Junonia lemonias, Junonia orithya, Kaniska canace, Leptosia nina, Neptis hylas, Pantoporia hordonia, Parantica aglea, Phalanta phalantha, Pseudozizeeria maha, Tirumala limniace, Ypthima baldus, Ypthima huebneri* and *Zizula hylax*.

Instantaneous sampling of focal individuals was used to record broad behavioural activities. At different locations in a plot, individuals encountered of target species were followed. During each focal follow, a single individual was followed for a maximum of five minutes and its activity was recorded every thirty seconds. The pursuit was stopped if the individual left the plot or was no longer visible. The four activities recorded were (1) flying: air borne, hovering; (2) feeding: inserting proboscis into a flower; (3) resting: stationary on a surface with wings closed; (4) basking: stationary on a surface in a sunlit patch with wings held open.

All-occurrences sampling on focal individuals was used to quantify behavioural events. During the focal follows described previously, all occurrences of chases (flying with or behind another individual) were recorded. Chases were used as a measure of interactions with conspecifics and heterospecifics.

Butterfly habitat use

To quantify differences between habitats in butterfly abundance and the number of different butterfly species using that habitat, each plot was divided into four quadrants and in each quadrant the number of butterfly species and butterfly abundance were measured through point samples. During a sampling session at a plot, at each point (one point per quadrant), the species identity of all the butterflies seen within a radius of 3 metres was recorded for a period of two minutes (the 3 m distance chosen based on the visibility in the plots and the period was kept short to minimise counting the same individual more than once). The data on species and individuals were pooled across the set of four point samples (one in each quadrant) to constitute one sample for a plot. Such samples were collected at different times of the day (0900 – 1700 hrs) for each plot. Approximately 114 hours of sampling effort were invested in behavioural and habitat use observations and yielded 513 focal follows for behavioural analyses and 73 samples for habitat-use analyses.

Plant diversity estimation.

Plant diversity in the study plots was measured in March 2012. The species identity of all trees and shrubs in each 30 × 30 m study plot was recorded. For small herbaceous plants, a central 5 m radius area was delineated within each study plot, and three 50 × 50 cm sub-plots were laid at random within this 5 m radius area. In the lantana-dominated habitat patches, the number of stems of lantana was counted in a central 5 × 5 m sub-plot within each 30 x 30 m study plot.

Analysis

In the behavioural analyses, first data from all species were pooled together and analysed. Behavioural activities—basking, resting, feeding and flying—were summarised as the proportion of scans in a focal follow for which that activity was recorded. The proportion of scans is a measure of the relative time spent in that activity and ranges from 0 to 1. Conspecific chase, an event, was summarised as chase rate—the number of chases recorded during a focal follow divided by the length of time of the focal follow and represented as chases per fifteen minutes. Since these behavioural data were not normally distributed, means and bootstrapped confidence intervals (calculated from 10,000 re-samples) are shown as descriptive statistics. Each of the four activities was analysed separately using a Generalised Linear Model (GLM) with binomial errors with the proportion of scans showing that activity as the response variable, and with forest type (SEF/MDF), lantana level (native, lantana-dominated), and an interaction between forest type and lantana level as predictors. Each focal follow was a data point in these analyses. Binomial errors were used as the response variable was a proportion (number of scans showing a particular activity out of a given total). As initial model-fitting indicated overdispersion, quasibinomial error structure was assumed and model coefficients were tested using the more conservative F tests (Crawley 2007). Model simplification through backwards deletion was carried out to arrive at the minimal adequate model (Crawley 2012). Chase rate was similarly analysed using a GLM with negative binomial errors, with the number of chases recorded during a focal follow as the response variable and the duration of the focal follow included as an offset to account for variation in sampling time. Species-wise analyses were not conducted because sample sizes for individual species across the different habitat and forest type categories under comparison were limited.

In the analysis of butterfly habitat use, (a) the number of different butterfly species recorded during a sampling session (species number), and (b) the number of individuals (all species together) recorded during a sampling session (abundance) were used as measures of the use of a habitat by butterflies. The data from individual point samples in each of the four quadrants in a plot for a given sampling session were pooled together to yield a data point (i.e., 4 point samples, one in each quadrant, constitute one data point). As the data on species number and butterfly abundance were not normally distributed, means and bootstrapped confidence intervals (calculated from 10000 re-samples) are shown as descriptive statistics. The number of butterfly species recorded during a sampling session was analysed using a GLM with Poisson errors (chosen as the response variable consists of counts). Forest type (SEF/MDF), lantana level (native, lantana-dominated), and the interaction between forest type and lantana level were included as predictors. Model simplification through backwards deletion was carried out to arrive at the minimal adequate model. Butterfly abundance (the number of individuals recorded during a sampling session) was similarly analysed in a GLM with negative Binomial errors (chosen because the abundance count data were overdispersed due to some samples with large values of abundance; Crawley 2012).

Note that in the behaviour and the species-number and abundance analyses, the individual data-point is a focal-animal sample or a point-sample session respectively, and not a plot. The plots were used to delimit representative habitat patches in which behavioural and habitat use observations were recorded. These analyses assume that the plots are a good representation of the larger forest and care was taken, by using previous information on species composition, to lay plots in habitat patches representative of the forest types and levels of lantana infestation. Care was also taken to invest substantial sampling effort to obtain robust sample sizes of butterfly behaviour and abundances in these plots (Table 2). The generality of inferences regarding association of behaviour and habitat use with lantana infestation and with forest type is well-supported because behaviour, species-number and abundance samples were obtained from three study

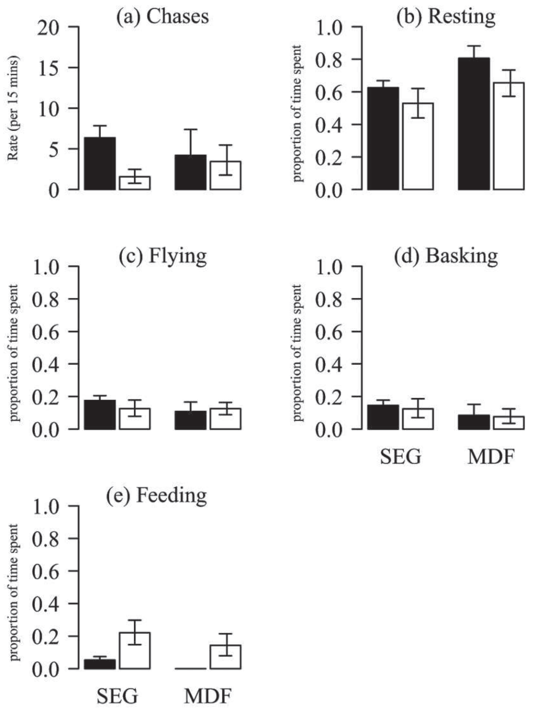

FIG. 1. Variation in butterfly behaviour between lantana-dominated habitat (white bars) and native vegetation with very little or no lantana (black bars) in the two forest types: frequency of chases (number of chases per 15 minutes) (a) and the proportion of time spent in resting (b), flying (c), basking (d) and feeding (e) activities. Error bars represent bootstrapped 95% confidence intervals.

patches for each category (three lantana-dominated vs. three native-vegetation plots and three MDF vs. three SEF respectively). However, the inferences regarding the interaction between lantana infestation and forest type are exploratory, since behaviour, species-number and abundance samples were obtained from only one habitat patch each of lantana-dominated habitat in SEF and native vegetation in MDF. Constraints in time and the area that could be covered during the study restricted the number of study plots. We checked whether our results were robust to potential non-independence in samples from a plot, by fitting generalised linear mixed-effects models (GLMM) with plot identity as a random effect to incorporate the repeated-measures structure in the sampling. Results from GLMMs were qualitatively similar and corroborated the main analyses. R software was used to analyse the data (R development core team 2011).

Shannon's diversity index was used to represent woody plant diversity (trees and shrubs pooled together) and herb diversity. Data from the three 50 × 50 cm quadrats within each 30 × 30 m study plot were pooled to calculate herb species richness, abundance and diversity for each study plot.

RESULTS

Behavioural analyses with all species pooled

Butterfly behaviour varied between the two forest types, and with the level of lantana infestation. Of the four behavioural activities, resting was most commonly seen and basking and feeding were relatively rare (proportion of focal follows with zeroes for feeding = 0.87, basking = 0.74, flying = 0.55, resting = 0.18, chase rate = 0.68; N = 513 focal follows).

Butterflies spent a lower proportion of time resting in lantana-dominated habitat than in native-vegetation habitat (GLM, F = 5.58, df = 1, P = 0.018, Fig. 1), and a higher proportion of time resting in MDF than in SEF (F = 16.82, df = 1, P < 0.005). The interaction between lantana and forest type was not significant (F = 0.16, df = 1, P = 0.685).

Butterflies spent a lower proportion of time flying in lantana-dominated habitat than in native vegetation (F = 4.16, df = 1, P = 0.041, Fig. 1), and a higher proportion of time flying in SEF than in MDF (F = 3.90, df = 1, P = 0.048), with no statistically significant interaction between lantana level and forest type (F = 2.11, df = 1, P = 0.146).

The proportion of time spent basking by butterflies was similar between lantana-dominated habitat and native vegetation (F = 0.08, df = 1, P = 0.077). The proportion of time spent basking was greater in SEF than in MDF (F = 6.30, df = 1, P = 0.012). The interaction between forest type and lantana level was not significant (F = 0.009, df = 1, P = 0.924).

Conspecific chases were fewer in lantana-dominated habitat than in native vegetation (χ^2 = 10.90, df = 1, P = 0.009, Fig. 1), and did not vary significantly with forest type (χ^2 = 0.09, df = 1, P = 0.756). The interaction between lantana and forest type tended to significance (χ^2 = 3.78, df = 1, P = 0.051), indicating that the difference in chase rate between lantana-dominated habitat and native vegetation may be greater in SEF than in MDF.

In contrast to the other behaviours, the proportion of time spent feeding was greater in lantana-dominated habitat than in native-vegetation habitat and this difference was larger in MDF as indicated by the statistically significant interaction between lantana level and forest type (F = 5.25, df = 1, P = 0.023)

Use of lantana-infested and native habitats by butterfly species

The number of species and the number of individuals seen during a sampling session were used as measures of the use of a habitat by butterflies. A total of 74 species was observed during the entire study. Of these, 65 species were recorded from SEF and 41 species were observed in MDF. A total of 58 species was observed in native-vegetation habitat and 43 species in lantana-dominated habitat.

The number of species seen during a sampling session varied with the level of lantana infestation and forest type. The number of species observed during a sampling session was greater in native vegetation than in lantana-dominated habitat (GLM, $\chi^2 = 4.191$, df = 1, $P = 0.041$) and greater in SEF than in MDF ($\chi^2 = 44.617$, df = 1, $P < 0.00001$, Fig. 2a).

Butterfly abundance during a sampling session was greater in native vegetation than in lantana-dominated habitat in SEF, whereas this difference was much smaller in MDF (GLM interaction term, $\chi^2 = 6.965$, df = 1, $P = 0.008$, Fig. 2b).

Plant diversity

Plant species richness for woody species (trees and shrubs) was roughly similar in lantana-dominated (range = 3–11) as well as native vegetation plots (range = 5–16) but the abundance of woody species differed greatly between these two habitats. In lantana-dominated plots, lantana was by far the most abundant woody species resulting in very uneven relative abundances of woody species. Accordingly, Shannon's diversity index was consistently higher for native vegetation plots (2.01–2.61) than for the lantana-dominated plots (1.4–1.6). Herb species richness and species diversity were also higher in native vegetation plots than in lantana-dominated plots (Table 2).

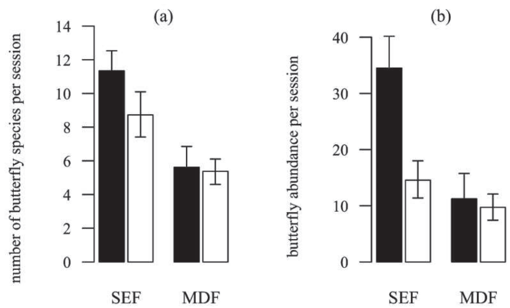

FIG. 2. Variation in butterfly habitat-use between lantana-dominated habitat (white bars) versus native vegetation with very little or no lantana (black bars) in the two forest types: comparison of the number of species (a) and butterfly abundance (b) recorded during a sampling session. Error bars represent bootstrapped 95% confidence intervals.

DISCUSSION

Our results from both behavioural observations and estimates of butterfly species numbers and abundances support the hypothesis that butterflies show reduced use of habitat patches dominated with the invasive weed, lantana, compared with patches with native vegetation. As expected, the proportion of time spent feeding was higher but the proportion of time spent in most other activities—resting, flying and conspecific interactions—was lower in lantana-dominated habitat. In addition, the number of species seen during a sampling session and butterfly abundances were lower in lantana-dominated patches. However, the differences in butterfly species-numbers and abundances were mainly seen in SEF. Taken together, these findings suggest a possible way in which an invasive plant may negatively affect native-butterfly assemblages: lantana by heavily infesting a habitat patch may reduce the resources and microhabitats important for different butterfly species. This can result in butterflies' obtaining only a part of their resources and habitat required for different activities in lantana-dominated habitats, consequently reducing their use of the invaded habitats.

Lantana infestation and butterfly behaviour

Several behaviours measured—resting, flying and conspecific interactions—were more commonly seen in native vegetation than in habitat dominated with lantana. Butterflies spent a higher proportion of time resting in native habitat. In native vegetation, butterflies (e.g., *Ariadne ariadne, Junonia iphita, Junonia lemonias, Pseudozizeeria maha, Ypthima huebneri*, and *Zizula hylax*), typically with cryptically-coloured hind wings, were seen resting on the ground or in the leaf litter, where they appeared well-camouflaged against the background; similar observations have been recorded for other butterfly species (e.g., *Vanessa atalanta*, Bitzer and Shaw 1979). It is possible that lantana-dominated habitat is not as suitable as native vegetation for crypsis as lantana forms a contrasting, thick, and almost continuous understorey vegetation cover that appears to be difficult to penetrate and find cryptic places for resting.

Chases, used as an indicator of species interactions, were similarly fewer in lantana-dominated habitat than in native vegetation. There are several possible reasons. First, if butterfly abundance is lower in lantana-dominated habitat (as we discuss below), perhaps because it is less suitable for activities, such as oviposition, encounter rates between conspecifics is likely to be reduced, resulting in fewer interactions. Second, more specifically, if these chases represent territorial behaviour (as seen in several previous studies; Baker 1972, Davies 1978), and if encounter rates with

TABLE 1. Description of vegetation in the study plots in the two forest types in BRT along with sample sizes for behavioural follows and habitat-use in 2011 and 2012. Sample sizes for behaviour (NB = Number of focal follows for measuring behaviour) and habitat use (NS = Number of sampling sessions for butterfly species-numbers and abundance) are also shown for each study plot in 2011 and 2012.

Plot No.	Forest type	Habitat type (Level of lantana cover)	Description	NB	NS
1	Semi-Evergreen	Native (Very little or no lantana)	Dominant trees: *Cipadessa baccifera, Elaeocarpus serratus, Ficus amplissima, Maesa indica, Randia* spp., *Syzygium cumini*, and *Terminalia bellirica*. Understorey: *Bidens pilosa, Cyanotis tuberosa, Desmodium repandum, Olea glandulifera, Sida rhombifolia*, and *Strobilanthes* spp	65 (2011) 87 (2012)	8 (2011) 12 (2012)
2	Semi-Evergreen	Native (Very little or no lantana)	Dominant trees: *Bombax ceiba, Grewia tiliifolia, Maesa indica, Phyllanthus emblica, Pterocarpus marsupium and Terminalia bellirica*. Understorey: *Adinoflora* spp., *Ageratum conyzoides, Cyanotis tuberosa, Desmodium repandum* and *Sida rhombifolia*.	80 (2011) 67 (2012)	9 (2011) 10 (2012)
3	Semi-Evergreen	Lantana-dominated (High lantana density)	Dominant trees: *Maesa indica, Persea macrantha* and *Viburnum punctatum*, Understorey: *Lantana camara*	43 (2011) 37 (2011)	7 (2011) 7 (2012)
4	Moist Deciduous	Native (Very little or no lantana)	Dominant trees: *Randia* spp., *Tectona grandis*, and *Terminalia bellerica*. Understorey: Grasses	50 (2012)	13 (2012)
5	Moist Deciduous	Lantana-dominated (High lantana density)	Dominant trees: *Randia* spp., *Solanaceace* spp., *Syzygium cumini*, and *Terminalia bellerica*. Understorey: *Lantana camara, Adinoflora* spp., *Bidens pilosa, Sida rhombifolia* and grasses.	48 (2012)	12 (2012)
6	Moist Deciduous	Lantana-dominated (High lantana density)	Dominant trees: *Mangifera indica* and *Terminalia bellerica*. Understorey: *Lantana camara, Bidens pilosa, Sida rhombifolia* and grasses.	36 (2012)	9 (2012)

females is low in lantana-dominated habitat for reasons such as those mentioned previously, then it may not be economical for males to invest in maintaining territories in such habitat. Butterflies spent a higher proportion of time flying in native vegetation and, although statistically not significant, the proportion of time basking was also different in the expected direction. Basking and feeding were relatively rare (see Results) and hence need further investigation to confirm observed patterns.

Feeding was the only activity on which butterflies spent a larger proportion of time in lantana-dominated habitat than in native vegetation. Lantana is known to be a nectar resource used by butterflies (Arévalo 2005, Schemske 1976, Kunte 2008) and since it is a dominant shrub flowering almost throughout the year (Kohli et al. 2006) it is likely to be an important nectar resource. The low proportion of time spent feeding in native vegetation could be due to the seasonality in the flowering of native herbs, shrubs and trees (Bhatt and Murli 2001). By feeding regularly on lantana, native butterflies may aid in lantana pollination and its spread in the area. This could negatively affect their populations if lantana displaces the remaining areas of native vegetation, which include larval host plants, but is not itself suitable larval host plants. On the other hand, lantana can act as an important nectar resource for adult butterflies. Invasive plants may not always influence native biodiversity negatively and positive influences on phytophagous insects have been described (Rodriguez 2006). The relative importance of these different potential processes by which an invasive plant, such as lantana, may influence butterfly behaviour and ecology is yet to be examined.

Butterfly behaviour also differed between the two forest types. Butterflies spent more time basking in SEF than in MDF and more time resting in MDF than in SEF. This pattern might be explained by the lower temperatures in the SEF (unpublished data) as a result of which butterflies might have to bask for longer to maintain optimum body temperature. Also, butterflies spent more time feeding in SEF than in MDF, perhaps because nectar resources are greater in the dry season in SEF than in MDF. In MDF, both native plants and lantana flowered throughout the study period, but showed comparatively lower levels of flowering than did SEF. These findings relate to one major season of butterfly activity during the year. Further work is needed to confirm whether these behavioural differences are also seen in the post-monsoon season, another period of substantial butterfly activity. Overall, our findings on butterfly behaviour in relation to lantana infestation suggest that lantana is commonly used as a food resource but may be less suitable for many other activities.

Lantana infestation and habitat use by butterflies. We predicted that because of the unsuitability of lantana-dominated areas for many butterfly activities, habitat use by butterflies should be lower in lantana-dominated areas than in native vegetation. We used butterfly abundance and the number of species recorded during a sampling session as two measures of butterfly habitat use. We find clear evidence for reduced butterfly abundance and reduced number of species in lantana-dominated habitat in SEF. The trend was similar in MDF but not as clear. There are several possible reasons for this difference between forest types: perhaps the butterfly community in MDF was more robust to habitat changes driven by lantana invasion compared with the community in SEF; alternatively, lantana extent may have been greater in MDF than in SEF, which may have already resulted in a reduced butterfly community in MDF, thereby depressing any difference in butterfly habitat use between lantana-dominated and native-vegetation patches within MDF; The total number of species and the average number of species seen during a sampling session was greater in SEF than in MDF, but how much of this difference reflects differences in lantana spread

TABLE 2. Vegetation patterns in the native and lantana-dominated study plots in the two forest types in BRT. Species richness, abundance, and Shannon's Index of diversity are shown for woody species and herbs. Tree abundance includes lantana stems in 30 x 30 m plots in lantana dominated plots. Sample sizes for behaviour (NB = Number of focal follows for measuring behaviour) and habitat use (NS = Number of sampling sessions for butterfly species-numbers and abundance) are also shown for each study plot.

Plot No.	Forest type	Habitat type (Level of lantana cover)	Tree Richness	Tree Abundance	Shannon's Index (Trees)	Herb Richness	Herb Abundance	Shannon's Index (Herbs)	NB	NS
1	Semi-Evergreen	Native (Very little or no lantana)	16	49	3.01	17	143	2.61	152	20
2	Semi-Evergreen	Native (Very little or no lantana)	11	29	3.15	10	103	2.1	147	19
3	Semi-Evergreen	Lantana-dominated (High lantana density)	11	253	0.31	7	40	1.5	80	14
4	Moist Deciduous	Native (Very little or no lantana)	5	15	1.4	9	28	2.01	50	13
5	Moist Deciduous	Lantana-dominated (High lantana density)	5	273	0.24	6	21	1.6	48	12
6	Moist Deciduous	Lantana-dominated (High lantana density)	3	233	0.07	5	22	1.4	48	9

and how much other ecological differences between the two forest types remains to be examined. While other studies have examined the effect of disturbance on butterfly diversity within a particular forest type (Hill et al. 1995; Spitzer et al. 1997), relatively few have examined how butterfly behaviour, habitat use and diversity vary between different types of forest within the same landscape.

Our results from comparing butterfly behaviour and habitat use in lantana-dominated and native-vegetation habitats suggest a mechanism by which an invasive plant may influence native butterfly assemblages. Lantana by dominating native habitat may reduce habitat heterogeneity and thus reduce the suitability of the habitat for native butterflies. For example, our behavioural findings suggest that lantana-dominated habitat is not as suitable as native vegetation habitat for several activities, including resting, flying and conspecific interactions. Furthermore, lantana-dominated habitat will inevitably have reduced larval host-plant abundance because lantana forms dense thickets displacing understorey vegetation, which include larval host plants, and lantana is itself apparently not used as a host plant. Larval host plants form an important part of the life cycle of butterflies and many aspects of adult butterfly habitat use (e.g., the search for oviposition sites by adult females, mate-searching and territorial behaviour) are closely linked to host-plant abundance. Our observations on plant diversity inside our study plots indicate that plant species diversity in lantana-dominated plots was lower than that in native vegetation plots. We do not have a comprehensive list of larval host plants from the study area, in part because most information regarding larval host plants is anecdotal for most Indian butterflies (Kunte et al. 2013). Thus, the reduced plant diversity in the lantana-dominated plots is likely to represent reduced host-plant abundance, which may have contributed to the reduced use of lantana-dominated habitat by adult butterflies in our study.

In the long term, a reduction in the use of lantana-dominated habitat could lead to a reduction in butterfly population sizes and ultimately butterfly diversity and abundance. While studies of butterfly behaviour in invaded and uninvaded habitat patches are scarce, studies of habitat use and populations, largely of temperate butterfly species report reduced habitat use (e.g., Severns and Warren 2008); reductions, even local extinctions in butterfly populations (e.g., Preston et al. 2012); and declines in diversity and abundance (e.g., Collinge et al. 2003, Moron et al. 2009, Valtonen et al. 2006) following the invasion of an area by exotic plants. Several of these studies link these reductions with a reduction in native plant abundance and diversity (Moron et al.2009), or more specifically with a decline in larval and adult resources (Preston et al. 2012, Severns and Warren 2008) as a result of the invasion.

Heavy infestation of areas is a characteristic for many invasive species (Newsom and Noble 1986); therefore, the process suggested by the findings from our study, that is, reduced habitat use by butterflies, as a result of lantana causing reduced resource and microhabitat abundance and diversity and corresponding poorer suitability for important activities, is likely to be general. Whether these local behavioural effects can lead ultimately to reduced population sizes and local extinctions will need to be examined.

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