

Assessing the synergistic effect of two invasive plants on native plant communities in Kanha National Park, Central India

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By

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SUMMARY

1. Over time, community assembly and functioning of native ecosystems is known to shift from native species to non-native species thus, restructuring the native community. When this shift of diverse native ecosystem interaction to less diverse invasive-centric interaction, occurs due to synergistic effect of two invasive species, it is known as '*invasional meltdown*'. Since last two decades, the effects posed by invasive species on ecosystems are widely debated. Studies across the globe have reported simplification in community structure with biological invasions, leading towards monotonous ecosystems and homogenization of biodiversity.
2. I assessed the interaction of two invasive plant species, *Lantana camara* complex (lantana) and *Pogostemon benghalensis* (pogostemon) with native understorey vegetation in *Shorea robusta* (Sal) forest of Kanha National Park, Central India. Here, I tested biotic homogenization, invasional meltdown and intermediate disturbance hypothesis. To achieve this, 56 km² out of 230 km² of Sal forest covering 5613 cells (100X100m) was extensively surveyed, to model species distribution of lantana and pogostemon using different correlative, mechanistic and ensemble models. From the surveyed area, 120 plots (10X10m) were selected based on the percent cover of invasive species, where vegetation and soil sampling was conducted. The correlations in community composition with edaphic and climatic parameters were established using non-parametric ordination, and the potential effects of single invasive species and their interaction were estimated using linear models by considering the uninvaded plots as control.
3. From the sampled area, 40 km² (71%) and 37 km² (66%) were found to be invaded by lantana and pogostemon respectively. Lantana presence was best explained as a function of nearby lantana density and was constrained by evapo-transpiration rate of summer, light availability and dry stress. Whereas, pogostemon presence was best explained by moistness of forest patch, lower summer temperature and habitat openings due to anthropogenic factors and was constrained due to climatic heat, edaphic dry stress, and remote deciduous forest.

4. I found that the plant species composition differed between uninvaded and invaded plots. A negative correlation of *Shorea robusta* was also found when lantana and pogostemon were present together. Linear Models established a significant decrease in native plant diversity and richness of rare plants (5.33 ± 0.10), with an increase in pogostemon (0.67 ± 0.29) and lantana abundance (0.50 ± 0.38). However, when both invasive species were present, a substantial decline in native species diversity, richness of rare plants (0.40 ± 0.36), soil moisture and an increase in species evenness, soil organic carbon and soil potassium was assessed.
5. Study results indicate an insignificant effect of intermediate disturbances, and significant impacts of invasive species on species composition and edaphic factors, thereby affirming the biotic homogenization and invasional meltdown hypothesis and rejecting intermediate disturbance hypothesis. Present study can be used as an evidence to prioritize immediate management interventions in areas where multiple invasions are present, as the chances of extirpation of rare species is high.

Keywords: Single invasion, multiple invasions, *Lantana camara*, *Pogostemon benghalensis*, invasional meltdown, biotic homogenization, species distribution models (SDM)



Field view 1: *Lantana camara* invasion on the banks of a stream bed in Kanha.

Background

In the very first episode of its second season, *Planet Earth*, one of the most popular web series showcasing global biodiversity, highlighted the synergistic effects of multiple species invasions on island ecosystem (BBC media centre, 2016). This popularity reflects the growing concern on biotic homogenization of the earth due to “*a few winners replacing many losers in the next mass extinction*” (McKinney & Lockwood, 1999); invasive species are one such winner. Invasive species are native or non-native species with established viable populations, which tends to modify the native ecosystem in a short span of time (Colautti and MacIsacc 2004, Blackburn et al. 2011). Biotic homogenization (Sax et al, 2005), reduction in biodiversity (Hejda et al. 2009, Shea and Chesson, 2002, Thelen et al., 2005), alteration in nutrient cycling (Wright et al., 2014, Sharma and Raghuvanshi, 2009) are some of the characteristics shown by them.

Release from controlling agents (enemy release hypothesis; Keane 2002), high phenotypic plasticity (Elton, 1958) and genetic diversity (Ray and Quader 2014) mostly help the invasive species to exploit essential resources. Invasive species alter the dynamics of invaded ecosystem and the interactions within the biotic and abiotic components of the invaded area (Green et al., 2011, Martin et al., 2009, Mcgrath & Binkley, 2009). Being opportunistic, they can sustain in limited amount of resources and induce changes in the soil chemistry, making it undesirable for native plants. Such allelochemicals are known to reduce the abundance and richness of native plants, at times resulting in local extinction. Dassonville et al. 2007 found invasion of *Fallopia japonica* (Japanese knotweed) increased top soil mineral contents by enhancing nutrient recycling rates leading to soil homogenization. Ehrenfeld et al. 2001 attributes changes in soil chemistry by *Berberis thunbergii*, a woody shrub, and *Microstegium vimineum*, a C4 grass, to decrease in native plant richness following exotic understory plant invasion. High magnitude of such changes can restructure the native ecosystem interactions to invasion centric interactions (Simberloff 2006). This restructuring due to synergistic effects of two invasive species can further facilitate other invasive species and magnify the impacts on native ecosystems, a hypothesis proposed as ‘*invasional meltdown*’ (Simberloff & Van holle 1999).

In last 10 years, studies testing invasional meltdown hypothesis have increased dramatically. The string search of ‘invasion* meltdown’ revealed 132 ecological studies published since 1999, 100 of which are published in last 10 years (Figure 1). Most of the studies affirmed that two or more invasive species can form a positive feedback within themselves that can substantially influence the native resources and species assemblage (studies confirming meltdown); while others rejected the hypothesis (rejecting meltdown). Studies that affirmed invasional meltdown, confirmed ‘biotic homogenisation hypothesis’ which states that *increased abundance and richness of invasive plants can homogenize the native plant community* (Sax et al. 2005). On the other hand, studies that rejected invasional meltdown, found that increased abundance and richness of invasive plants had no impact on the native plant community (Wyckoff 2014). Such results can potentially be a subset of larger community pattern, where “*diversity of competing species should be expected to be, maximized at intermediate frequencies and/or intensities of disturbance or environmental change*”, also known as ‘intermediate disturbance hypothesis’ (Connell 1978). However, beyond the threshold, plant communities are mostly expected to homogenize.

These changes in community patterns depend upon the involved invasive-invasive and invasive-native interaction (Simberloff 2006). For example, competition (nutrient uptake, exudation of novel chemicals (Cappuccino & Arnason 2006)) within two invasive plants was found to modify the native plant composition (Hughes et al., 1991, Gioria and Osborne 2011). However, effects of an invasive plant on native plant richness have been studied (Psyek et al., 2012). But, a holistic comparison of different gradients of invasions (from no invasion to multiple invasions) with the available resources, native common species assemblage and native rare species assemblage is limited, which the present study aimed at.

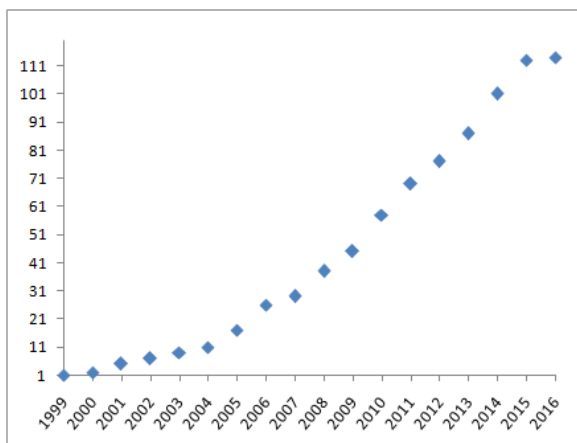


Figure 1: Cumulative increase in studies (n=132) reporting invasional meltdown hypothesis, since 1999 when the hypothesis was proposed. The search was made in ‘Web of Knowledge’ using a search string ‘invasion* meltdown’.

For this, I first estimated the densities of *Lantana camara* complex (Lantana, henceafter), an introduced species, and *Pogostemon benghalensis* (Pogostemon, henceafter), a native weed, through extensive sampling in the *Shorea robusta* (Sal, henceafter) forest of Kanha National Park in Central Indian landscape. I derived Species Distribution Maps (SDMs) and tested correlative and mechanistic models to predict their presence and absence. From the surveyed area, 120 plots of 10X10m each were selected based on the cover of invasive species, to record abundance of native and invasive plant species. I calculated diversity parameters like species richness, species evenness and Shannon-Weaver diversity index and assessed plant community structure and composition using non-metric multidimensional scaling (NMDS) and Canonical Correspondence Analysis (CCA).

Both species, being opportunistic are expected to extract nutrients from the top soil level, thereby altering with the soil nutrient composition. With this change in soil chemistry, native plant richness is expected to decrease with the increasing abundance of the invasive plants. In the present study, I also tested invasional meltdown hypothesis (Simberloff and Von Holle 1999), intermediate disturbance hypothesis (Connell 1978) and biotic homogenisation hypothesis (McKinney and Lockwood, 1999) for invasion of lantana and pogostemon using linear models.



Field view 2: Morning view of open *Shorea robusta* forest invaded with *Lantana camara* and *Pogostemon benghalensis*.

The Question

To test Invasional meltdown hypotheses, Biotic homogenization hypothesis and Intermediate disturbance hypothesis, the following objectives and research questions were studied:

Objective 1: To estimate the distribution and density of *Lantana camara* and *Pogostemon benghalensis* in Sal forest of Kanha National Park.

Research question:

1. *How are Lantana and Pogostemon distributed in sal forest of study area?*
2. *Which environmental parameters explain their presence and absence?*

Objective 2: To assess the difference in plant species composition along the gradient of plant invasion.

Research questions:

1. *Is there a difference in species composition of invaded and uninvaded areas?*
2. *What is the relationship between environment and plant community in the study area?*
3. *What is the difference in species richness, diversity, evenness of native plants and edaphic factors across the plant invasion gradient?*



Field view 3: *Pogostemon benghalensis* invasion along the bank of a stream in Kanha.

Study area and design

The present study was conducted in Kanha National Park in Madhya Pradesh. Kanha NP is a part of central Indian highlands and extends from 22° 02' 52" N to 22° 25' 49" N and 80° 30' 09" E to 81° 02' 49" E. This 940 km² broad area has a mosaic of four major forest type viz. *Shorea robusta* dominated forest, *Shorea - Terminalia* dominated miscellaneous forest, bamboo forest and grasslands. Kanha harbours a wide range of flagship species and endangered species, some of which are Tiger (*Panthera tigris tigris*), Gaur (*Bos gaurus*), Wild dog (*Cuon alpinus*), Barasingha (*Rucervus duvaucelli branderi*), Vulture (*Gyps* sp.). Apart from native plants, the area also has numerous weed species like *Senna tora*, *Lantana camara*, *Pogostemon benghalensis*, *Parthenium hysterophorus*, *Ageratum conyzoides*, *Hyptis suaveolens* etc. that are known to affect the habitat of endangered flagship species in the park (Management plan, 2010).

Taking into consideration, objectives of the study and diverse habitat types of Kanha NP, *Shorea robusta* (Sal) dominated forest in the four western ranges (i.e, Kisli, Kanha, Mukki and Sarhi) was selected to be the intensive study area. Rationale behind this selection was to minimize the innate variability in plant understorey composition caused due to heterogeneous forest type. Selected ranges in the study area also share similarity in weather conditions, moisture regime and management timeline. Although, the other two ranges, namely, Supkhar and Baisanghat, hold good percentage of Sal dominated forests but are relatively moister, hilly (undulating), dissimilar in weather conditions, because of which they were excluded from the current study.

METHODS:

For objective 1: A map of drier *Shorea robusta* (sal) forest of Kanha National Park (geographically located in the Kanha, Kisli, Mukki and Sarhi forest ranges of the park) was obtained from the Management plant (2010). The forest was divided virtually in a grid of 100X100m using a GIS domain. 1 or 2 non-overlapping straight transects of 2 km (Fig 3A) were walked in the sal forest of every beat (an administrative unit of the forest department, 15-20 km²) in the study area. At every 100m, a perpendicular distance of 200 m (Fig 3B) to transect was walked along which five plots of 15m radius were sampled at every 40 m distance. At these plots another perpendicular

distance of 40m (Fig 3C) was walked on both the sides and a plot was sampled. At each plot, percent cover of all the invasive plants, ocular canopy cover, and number of native trees were recorded. In addition to this, trail walks and vehicle surveys were also conducted in the study area, where, at every 40m a 15m radius plot was sampled (in case of vehicle transect, the plot was away from the road) to record the percent cover of invasive plants. On an average, every cell of 100X100 m had 3 plots (range 2-7), covering 22% area of the grid. In total 5613 grid cells were sampled, covering 56 km² of the 231 km² Sal forest in the study area.

Remotely sensed data was used to index the bioclimatic parameters. Annual temperature, temperature of warmest and coldest month, precipitation of wettest quarter was used from the WorldClim database (Fick & Hijmans 2017). Land surface temperature was further derived as an index of soil surface temperature using the band 10 and band 11 of the summer (April 2017) image of Landsat 8. NDVI was derived from the same image as well as image of post-monsoon (November 2016) as an index of vegetation cover. Soil moisture data procured from the SMAP (Soil Moisture Active Passive) was used as an index of soil moisture. Sal forest map was used for calculating Euclidean distance from the edge to the centre of each patch. I also derived a layer of Euclidean distance from tourism roads, forest clearings used as fire lines and water bodies as an index of canopy openings. All of these layers' information was averaged and attached to the 100x100 m² grid using ArcMap 10.2. Source and resolution of the remotely sensed data is provided in the Appendix S1 C.

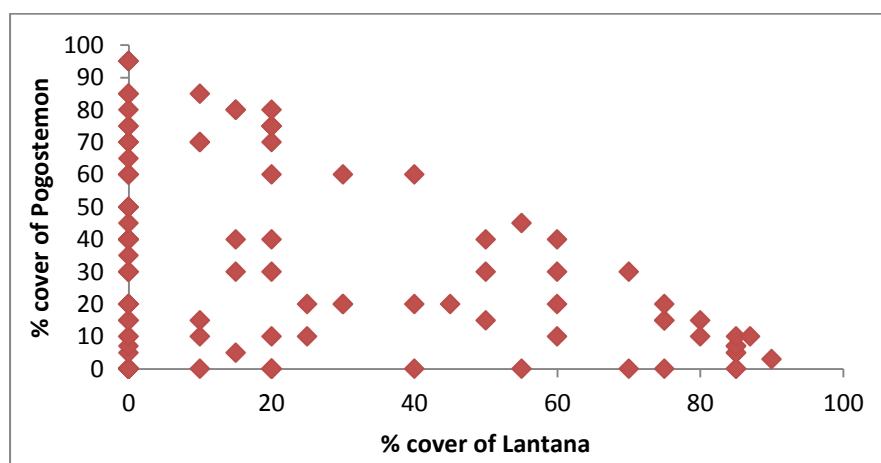


Figure 2: Arrangement of 120 sampling plots in the increasing magnitude of lantana and pogostemon.

Table 1: Invasion matrix showing thirteen classes of invasion, based on the % cover of lantana and pogostemon. Number in brackets indicates the number of sampling plots for every invasion category.

	Invasive Plant 1 (<i>Lantana camara</i>)				
		No	Low (10-30%)	Medium (40-60%)	High (70-100%)
Invasive plant 2 (<i>Pogostemon benghalensis</i>)	No	NPNL (15)	NPLL (04)	NPML (04)	NPHL (04)
	Low (10-30%)	LPNL (06)	LPLL (11)	LPML (06)	LPHL (15)
	Medium (40-60%)	MPNL (16)	MPLL (05)	MPML (04)	
	High (70-100%)	HPNL (12)	HPLL (08)	Demographically does not exist	

For objective 2:

From the surveyed area of 56km², 120 plots (10X10m each) were further selected, to intensively record the biological aspects of both the species, and native vegetation structure. The sampling was based along the increasing magnitude of plant invasion, where both the invasive species were categorized with respect to their percent cover (Absent, low, medium and high abundance; Figure 2). Thirteen classes which differed in the abundances of both the invasive species were thus formed (Table 1).

In these sampling plots, all the native trees and shrubs were recorded (Jhala et al., 2013). Species were identified using Krishen 2013 and Madhya Pradesh vegetation list (Jhala et al, 2015). Along with the data on species and their abundance, data on phenology and height of trees and shrubs was collected (Appendix S1 A, B).

Three subplots of 1m×1m were also laid in every sampling plot where, all the herbs and grass species and their abundance were noted. Ocular estimation of litter cover, herb cover, grass cover and bare ground (in percentage) was also done, Litter depth was noted by using a ruler and light penetration on ground was also noted down (Jhala et al., 2013).

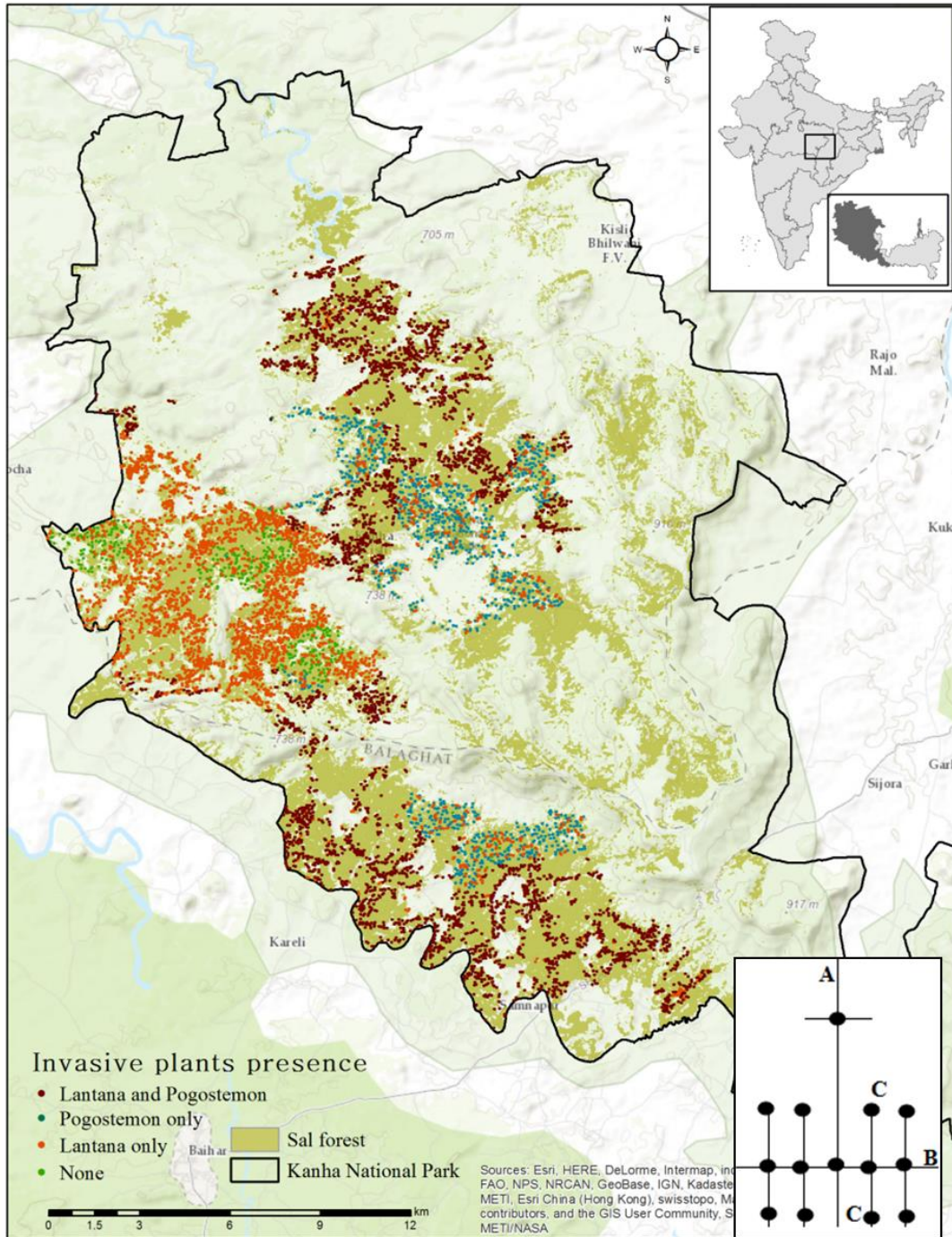


Figure 3: Plots surveyed across the Sal forest in the study area to record the abundance of lantana (red), pogostemon (blue), both (maroon) and none (green). Inserted map on the top right corner shows the geographic location of study area in the Kanha National Park, Madhya Pradesh, India. Survey design where transect (A) and perpendicular to it (B, C) were walked to sample the plots (black points).

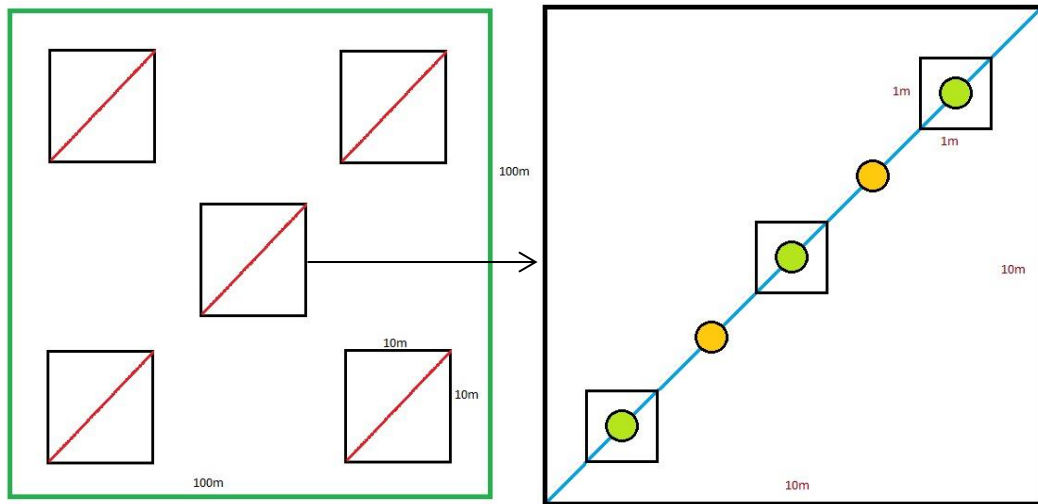


Figure 4: (a) Alignment of sampling plots in a 100 X100m grid, (b) A sampling plot with arrangement of 1 X1m sub plots.

At every plot three samples (150g each) of soil were collected and stored for further analysis. Canopy cover was visually estimated from three different points in the plot. Number of lantana and pogostemon seedlings (< 15cm height), saplings (15-50cm) and grown plants (> 50cm) were recorded at every plot.

In order to minimize the effect of linear forest infrastructure (forest roads and fire control lines), grasslands, waterbodies (streams and lakes) and other forest type, sampling plots were laid at a minimum distance of 300 m from them. To minimize the effect of terrain structure and complexity on sampling outcomes, terrain type was also restricted to flatter areas.



Field view 4: Field staff indulged in vegetation and habitat sampling.

Lab methods

Soil analysis: The collected soil sample was spread out on a tray and left for air drying in the field and the dried sample was then weighed by using a digital weighing scale. The dried sample was then sieved using a 2mm sieve.

For analysing soil moisture, sample was weighed and put in the oven for twelve hours at 105⁰ C. The sample was then cooled down to room temperature and weighed again.

$$\text{Moisture content (\%)} = ((\text{Weight}_{\text{wet}} - \text{Weight}_{\text{dry}}) \times 100) / \text{Weight}_{\text{dry}}$$

Walkeley and Black (1934) was followed to estimate Organic Carbon content in the soil sample. Estimation of Phosphorus was done by following Bray and Kurtz, 1945 and Potassium by following Hanway and Heidel 1952.

Statistical analysis

Mechanistic models

Biophysical threshold modelling (BTM) - The genus lantana and pogostemon comprise of tropical shrubs with high phenotypic plasticity and genetic diversity (Ray & Ray 2014, Ray and Quader 2014). However, species at local scale are known to be influenced by micro-climate and hence, I assume them to respond to the present subset of their fundamental niche. Being plastic as well as ruderal species, I assume both the species to grow on range of soil fertility, excluding barren rocks, steep cliffs and water bodies. I calculated species' water requirement as function of their thermoregulation and body mass. I determined the average transpiration through plant surface to account for water lost in thermoregulation, and added this amount to the total body water requirement. This water requirement of both the plants was calculated as a function of area (1-hectare) and average annual precipitation. Both, lantana and pogostemon are known to grow with minimal light available, but during sampling period they were observed to not occupy areas where the native canopy was dense (>0.4). As both species can germinate across the year, I extracted the average temperature within the range of species' germination temperature, while the germination moisture is known to be present across tropical India. I further used the areas below heat, cold, dry and wet stress threshold of both the species by correlating the sampled information from 120 plots with the remotely sensed data. These physiological, reproductive and stress parameters range for both the plants across the sampling were added together. High

scores represented high probability of species occurrence while low scores represent species' absence.

Biophysical Density Modelling (BDM) - As both the study species grow as thickets and are known to spread in a way, where the thicket at centre is densest and gets rarer away from the centre, which might be attributed to the vegetative propagation of these species. I used the average densities of lantana and pogostemon in the 1-hectare grid as a basic source of information on species density distribution. I further produced 100 simulations of densities based on these training grids using the empirical Bayesian kriging (Krivoruchko 2012) that corrects for the error introduced by estimating the underlying semi-variogram. I rejected all the predicted densities where the standard error of density was higher than the mean density probability of lantana or pogostemon. I used the density surface for each species as a weight to the BTM to produce a biophysical density model of lantana and pogostemon.

Correlative models

Linear modelling (LM) - I modelled averaged percent cover of species within a grid cell, as a linear function of environmental covariates. I first z-transformed (Zar, 1989) the covariates for every species and inputted all the covariates for linear regression modelling. Later, I modelled the species percent cover as a function of uni-model and different combinations of climatic, edaphic and disturbance covariates. The most parsimonious combination with highest classification accuracy was considered as the best model. I used Akaike information criterion (AIC) for assessing the accuracy of each model. Model with least AIC was considered as the best explanatory model of species density (Johnson & Omland 2004).

Occupancy modelling (OM) - I explicitly account for detection bias by modelling and correcting for detection probability of species on our sampled plots (MacKenzie et al., 2002). Further I modelled species occurrence with covariates as a logit - link function (MacKenzie et al., 2002, Hines 2006). Z-transformed covariates were first used one at time as a logit – link function to model occupancy. Covariates that significantly improved the model were retained. I further combined these significant covariates to parsimoniously explain occupancy. Similar to LM, AIC was used for assessing these univariate and multivariate models, and model with least AIC was considered as the best explanatory model of species occupancy.

Maximum Entropy (MaxEnt) - MaxEnt takes species presence locations as input and sample background locations to contrast the environmental predictors and produce a probability distribution that represents a set of constraints (environmental variables) derived from the occurrence data. The most unconstrained model developed is considered as the MaxEnt model (Phillips & Dudik, 2008). In the present study; linear, quadratic and threshold features of MaxEnt were used with 10,000 background points and 100 replicates. To correct the bias due to unequal sampling of every grid, I calculated number of sampling plots in every cell as an index of sampling intensity. This was used as a bias grid in MaxEnt. MaxEnt produces niche probability for every pixel that varies from 0 to 0.99. In the present study, all pixels above 10 percentile training presence of the output raster were considered to be potential presence, as it is considered as a robust cut off from previous studies (Elith 2010). I further compared species-environment relationship derived from MaxEnt model that uses presence-background information with a model that uses presence-absence information. Other model settings were kept constant. Model with highest Area under the Curve (AUC) was considered as the best explanatory model explaining the presence of species (Hosmer & Lemeshow, 1989).

Model validation - I relied on 3 indices to compare model results with the species presences that are not used for model building; sensitivity index, specificity index, and variation index. Sensitivity index in the true presences predicted divided by the total number of true presences (%+), while the same proportion for true absences is the specificity index (%-) (Manel et al., 2001). Overall model performance (%*) was calculated by adding the above two index divided by the total presence and absence (Manel et al., 2001).

Ensemble - I ensembled (EM) the 5 SDMs used (BTM, BDM, LM, OM, MaxEnt,) based on the specificity and sensitivity of each model (Araujo & New 2006). For this, I estimated the overall sensitivity and specificity of all models together, and the relative sensitivity and specificity was derived by dividing the model sensitivity and specificity by overall sensitivity and specificity. If the site was predicted as presence, product of the relative sensitivity and modelled site probability was calculated. Similarly, if the site was predicted as absence, relative specificity was used. These product values were added for a site for all models and divided by the sum of used relative sensitivity and specificity. This produced an ensembled prediction for

every site, where probability greater than 0.5 was considered as presence, else absence. I further, calculated the sensitivity, specificity and overall performance for the ensemble model. As the BDM is based on exclusive density which might outfit other models, I modelled another ensemble (EM-BDM) with only 4 SDMs (BTM, LM, OM, MaxEnt) and validated the model in similar way. Statistical and GIS analysis was performed using R. 3.0.2 and ArcMap 10.2 respectively.

Diversity parameters:

With the collected information, ‘*Species accumulation curves*’ and ‘*Rank abundance plots*’ (RA) were generated using Microsoft excel 2010, for all the vegetation strata. RAs were generated to infer commonness, rarity and evenness for 13 different categories of invasion (Appendix S2 A). Measures of diversity like species richness, Shannon diversity and species evenness were also calculated for each sampling plot using R.3.0.2.

NMDS: To visualize the difference in community ordination between species and 120 sampled sites, non-metric multidimensional scaling (NMDS) was used. For plotting NMDS on the species-sites matrix, Bray-Curtis dissimilarity matrix was calculated (distance = "bray"). The rationale behind the selection of Bray-Curtis index was that this index is based on “*the sum of the differences in attributes between each pair of sites divided by the sum of the attributes for the pairs of sites*” (Abreu and Durigan 2011). Species abundance data was used from each plot with four divisions Native (uninvaded plots), Lantana (plots invaded with Lantana only), Pogostemon (plots invaded with Pogostemon only), L+P (plots invaded with both the species).

The NMDS was calculated with the VEGAN package in R (Oksanen et al. 2009), which aims to find a stable solution using several random starts. To find a stable solution, 50 permutations (trymax = 50) and 3 axes (k = 3) were selected for the analysis. All the data analyses were made in R 3.0.2 (R Development Core Team 2009).

CCA: After visualising the invaded and uninvaded plots in NMDS, Canonical Correspondence Analysis (CCA) was done to relate the distribution of plant species composition with the environmental predictors (Guisan et al. 1999, Braak 1987). CCA was performed using BiodiversityR package in R 3.0.2 (Kindt and Kindt 2016). A total of 1000 permutations were set and environmental variables which explained

maximum proportion of variance were selected for the analysis (Abundance of Pogostemon (PogoAbun), Abundance of Lantana (LanAbun), Soil moisture (Smoist), Light on ground (lightGr), land surface temperature of April (ran_aprlst) and deciduousness of the forest (ran_ndvidi)).

Comparing response variables along the gradient of plant invasion using linear model (ANOVA)

To establish the correlation of lantana and pogostemon abundances with diversity parameters and soil nutrients, native species richness, richness of rare species, Shannon-Weaver diversity, evenness, organic carbon, potassium and soil moisture content (response variables) were calculated for 120 sampling plots. Difference in the response variables for plots with single and multiple invasions as compared to native plots were estimated using the Linear Models (LMs) in ANOVA framework (Werts and Linn 1970, Bolker 2008). Thus, un-invaded plot (NPNL) was taken as contrast or reference plot, against which the beta values for each plot represented the degree of variation and p-value represented the significance of it. These response variables were assessed for multicollinearity and checked for pearson's correlation. The analyses were computed in R. 3.0.2.

Field view 5: Prof Qamar Qureshi and Dr Y.V.Jhala visiting a sampling plot in a low lantana abundance area.



Distribution of Invasive plants

Out of the 56 km² surveyed area, 40 km² (71%) and 37 km² (66%) was found to be invaded by lantana and pogostemon; while, 14 km² (29%) and 20 km² (34%) was devoid of their invasion, respectively. Results of 120 plots intensively surveyed for understanding the physiological parameters, germination success and environmental stress are summarized in table 2.

Lantana camara complex:

Mechanistic models: BTM best explained lantana presence to be constrained by evapotranspiration rate of summer (<130 mm/day), light availability and dry stress (< 37°C); as other constrains did not limit the study area. It could only classify 53% of presence and 29% of absence of lantana. BDM on other hand best explained lantana presence as a function of nearby lantana density, and then, by constrains explained by BTM. BDM could classify 94% of lantana presence and 97% of its absence in the study area.

Correlative model: LM best explained lantana cover to increase with increase in summer temperature, Annual temperature, deciduousness of forest and decrease with distance from canopy opening and forest patch edge. It could classify 95% and 13% of lantana presence and absence, respectively. OM best explained lantana presence to increase with increase in summer temperature, Annual temperature, deciduousness of forest, distance from forest patch edge (insignificant) and decrease with distance from canopy opening and post-monsoon NDVI. OM could classify 97% presence and 16% absence of lantana. MaxEnt best modelled lantana presence with increase in summer temperature, Annual temperature, deciduousness of forest, distance from forest patch edge (insignificant) and decrease in distance from canopy opening and post-monsoon NDVI. It could classify 76% and 28% of lantana presence and absence. Relative importance of the environmental covariates for explaining lantana presence in LM, OM and MaxEnt is summarized in table 3. However the explanatory power of LM and OM was low (LM R² value =0.18, OM R² value=0.13), while that for MaxEnt was

relatively higher (AUC=0.59). Details on stepwise selection of different models for each correlative SDM is provided in the Appendix S1 D.

Table 2: Physiological parameters, germination success and environmental stress threshold of lantana and pogostemon in the study area; used for deriving the mechanistic model of species.

Mechanisms	Lantana	Pogostemon	Source
<i>Physiology</i>			
Body water content (g)	748 (18-1953)	554 (40-1403)	Present study
Body temperature (°C)	29 (22-38)	25 (21-33)	Present study
Evapotranspiration threshold (mm/day)	< 130	< 95	Present study
<i>Germination</i>			
Germination temperature (Annual average temperature(°C))	22 (15-38)	19 (16-33)	CABI
Germination moisture	throughout	throughout	CABI
Light (canopy density)	NDVI < 0.40	NDVI < 0.43	Present study
<i>Stress</i>			
Heat stress (Maximum temperature of warmest month (°C))	> 41	> 40.5	Wijayabandara et al 2013
Cold stress (Minimum temperature of coldest month (°C))	< 5	< 5	Wijayabandara et al 2013
Dry stress (Soil surface temperature (°C))	>37	>33	Present study
Wet stress (maximum rainfall of the wettest month (mm))	>1195	>1280	Present study

Ensemble model: Presence and absence of lantana was best modelled by EM, with a very little improvement as compared a mechanistic model BDM (Table 5). Ensemble model with BDM removed had higher discriminatory power as compared to any other non-BDM model. Thus I considered lantana distribution modelled by best fit model - BDM. As estimated from the BDM, lantana invaded 70 (63-229) km² in the study area (fig 5).

Pogostemon benghalensis

Mechanistic models: BTM best constrained pogostemon presence by heat (<40.5 °C) and dry (<33 °C) stress, germination temperature (<33 °C), and evapotranspiration rate during summers (< 95 mm/day). BTM classified 63% presence and 70% absence of pogostemon. BDM best explained pogostemon presence with information on the nearest density of pogostemon; and secondly by the BTM parameters. It classified 94% and 95% of pogostemon presence and absence.

Table 3: Relative contribution of different environmental parameters to explain the presence or absence of lantana in study area in different correlative SDMs.

Model parameters	LM β coefficient (±SE)	OM ψvalue (±SE)	MaxEnt %Contribution
Detection coefficient	NA	2.42 (±0.08)	NA
Intercept	30 (±0.43)	1.65 (±0.07)	NA
Summer temperature	4.73 (±0.51)	0.26 (±0.06)	13.9(±2.5)
Annual temperature	1.36 (±0.43)	0.14 (±0.05)	5.1(±0.8)
Distance inside forest patch	-4.6 (±0.51)	0.01 (±0.05)	4.6(±0.3)
Distance from canopy openings	-8.91 (±0.42)	-0.46 (±0.04)	15.3(±2)
Post-monsoon NDVI	NA	-0.51 (±0.01)	3.1(±0.5)
Moistness of forest	-3.04 (±0.42)	-0.51 (±0.01)	58.1(±10.6)

Correlative models: LM best explained pogostemon percent cover with increase in moistness of forest and decrease in summer and annual temperature and distance from canopy openings. It classified 96% presence and only 7% absence of pogostemon. OM best explained pogostemon presence with increase in moistness of forest, post-monsoon NDVI, and decrease with summer and annual temperature and distance from

canopy openings. It classified 88% and 19% of pogostemon presence and absence. While, MaxEnt modelled pogostemon presence with increase in moistness of forest, post-monsoon NDVI, and decrease with summer and annual temperature and distance from canopy openings and patch edge. It could discriminate 90% presence and 23% absence of pogostemon. Relative importance of these covariates for explaining pogostemon presence is summarized in table 4.

Ensemble model: Pogostemon presence and absence was best discriminated by ensemble models (94% presence and 95% absence; Figure 6). EM-BDM lost its discriminatory accuracy when density information was removed from it (52% presence and 67% absence).

Table 4: Relative contribution of different environmental parameters to explain the presence or absence of pogostemon in study area in different correlative SDMs.

Model parameters	LM β coefficient (±SE)	OM ψ value (±SE)	MaxEnt %contribution
Detection coefficient	NA	3.28 (±0.12)	NA
Intercept	38.4 (±0.49)	0.82 (±0.04)	NA
Summer temperature	-6.76 (±0.59)	-0.79 (±0.05)	19.1(±3.2)
Annual temperature	NA	NA	0.5(±0.1)
Distance inside forest patch	-4.82 (±0.59)	-0.46 (±0.04)	9.1(±1.7)
Distance from canopy openings	-3.6 (±0.49)	-0.33 (±0.04)	4.3(±0.6)
Post-monsoon NDVI	NA	0.45 (±0.14)	0.5(±0.1)
Moistness of forest	18.52 (±0.49)	0.45 (±0.14)	66.5(±11.2)

Table 5: Comparing the discriminatory power of SDMs for differentiating species' presence and absence using the sensitivity index (%+), specificity index (%-) and model performance (%*). Darker shade represents stronger index. Area estimated to be invaded by each SDM is given separately.

Model	<i>Lantana camara</i>				<i>Pogostemon benghalensis</i>			
	%+	%-	%*	Area (km ²)	%+	%-	%*	Area (km ²)
LM	0.95	0.13	0.69	212	0.96	0.07	0.65	220
OM	0.97	0.16	0.74	229	0.88	0.19	0.71	225
MaxEnt	0.76	0.28	0.74	221	0.90	0.23	0.89	176
BTM	0.53	0.29	0.52	139	0.63	0.70	0.64	124
BDM	0.94	0.97	0.95	63	0.94	0.95	0.95	69
EM	0.95	0.95	0.95	70	0.94	0.95	0.95	79
EM-BDM	0.75	0.59	0.71	148	0.52	0.67	0.57	92



Field view 6: Early morning visit to sample Sal forest for cover of invasive plants.



Figure 5: Lantana distribution modelled by Linear Model (LM), Occupancy Model (OM), Maximum Entropy (MaxEnt), Biophysical Threshold Model (BTM), Biophysical Density Model (BDM) and Ensemble of all these models (Ensemble) in the study area



Figure 6: Pogostemon distribution modelled by Linear Model (LM), Occupancy Model (OM), Maximum Entropy (MaxEnt), Biophysical Threshold Model (BTM), Biophysical Density Model (BDM) and Ensemble of all these models (Ensemble) in the study area.

Species composition and community structure

For the present study, species accumulation asymptotes were reached for all the vegetation taxa being studied. A total of **42** tree species, **65** shrub species, **38** herb species and **11** grass species were recorded during the field work. For trees, shrubs, herbs and grasses, the species number accumulated after **99**, **105**, **102** and **77** plots, respectively.

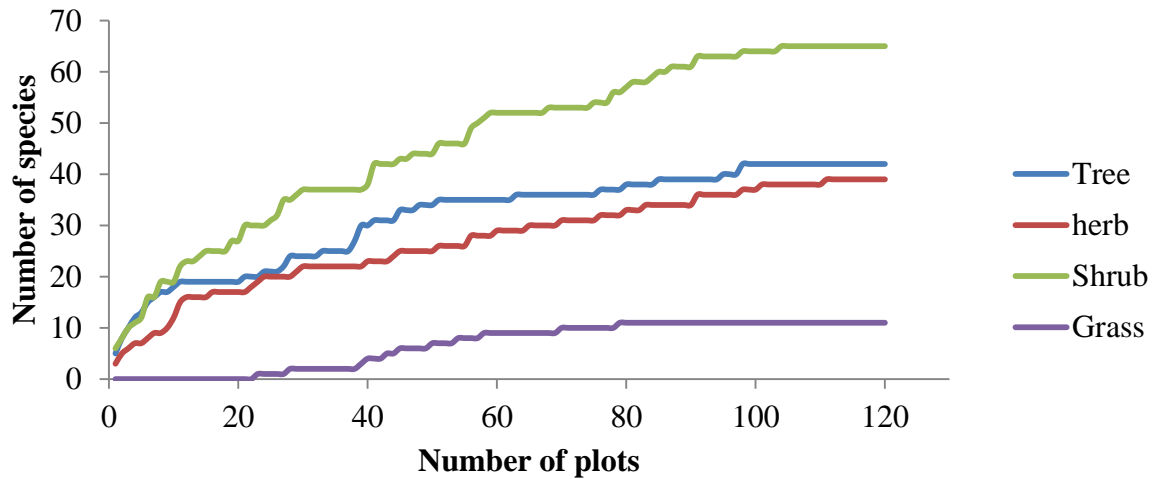


Figure 7: Species accumulation curve for trees, shrub, herbs and grasses.

The generated Rank abundance plots provide basic information about the relative abundance of species in the community. Species that occurred in 12 sampling plots (10% of 120 sampling plots) or lesser were considered as rare species for the study area (Appendix S5).

The NMDS community ordination divided the sampled plots and species on the basis of their observed dissimilarities (Figure 9). A clear difference was derived between native and invaded community (Kruskal stress value of 0.19). Differences in community composition between non-invaded and invaded plots were largely described by scores from the third NMDS axis, where all the uninvaded plots gained similar loadings and formed a cluster. Observed dissimilarity between the plots was explained by the ordination distance (Non-metric fit; R square value = 0.963) (Figure 8).

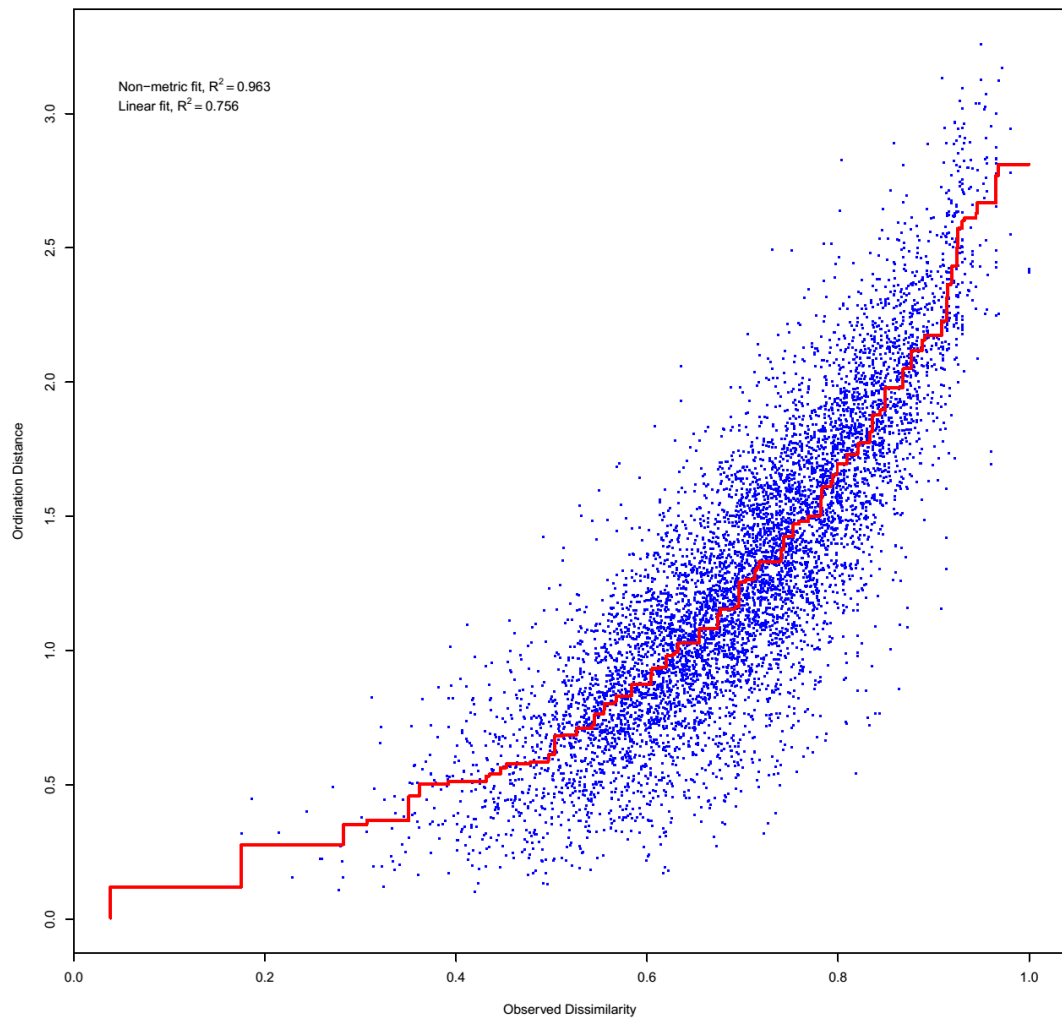


Figure 8: Stress plot for Non-metric multidimensional scaling (Non metric fit, $R^2=0.963$).

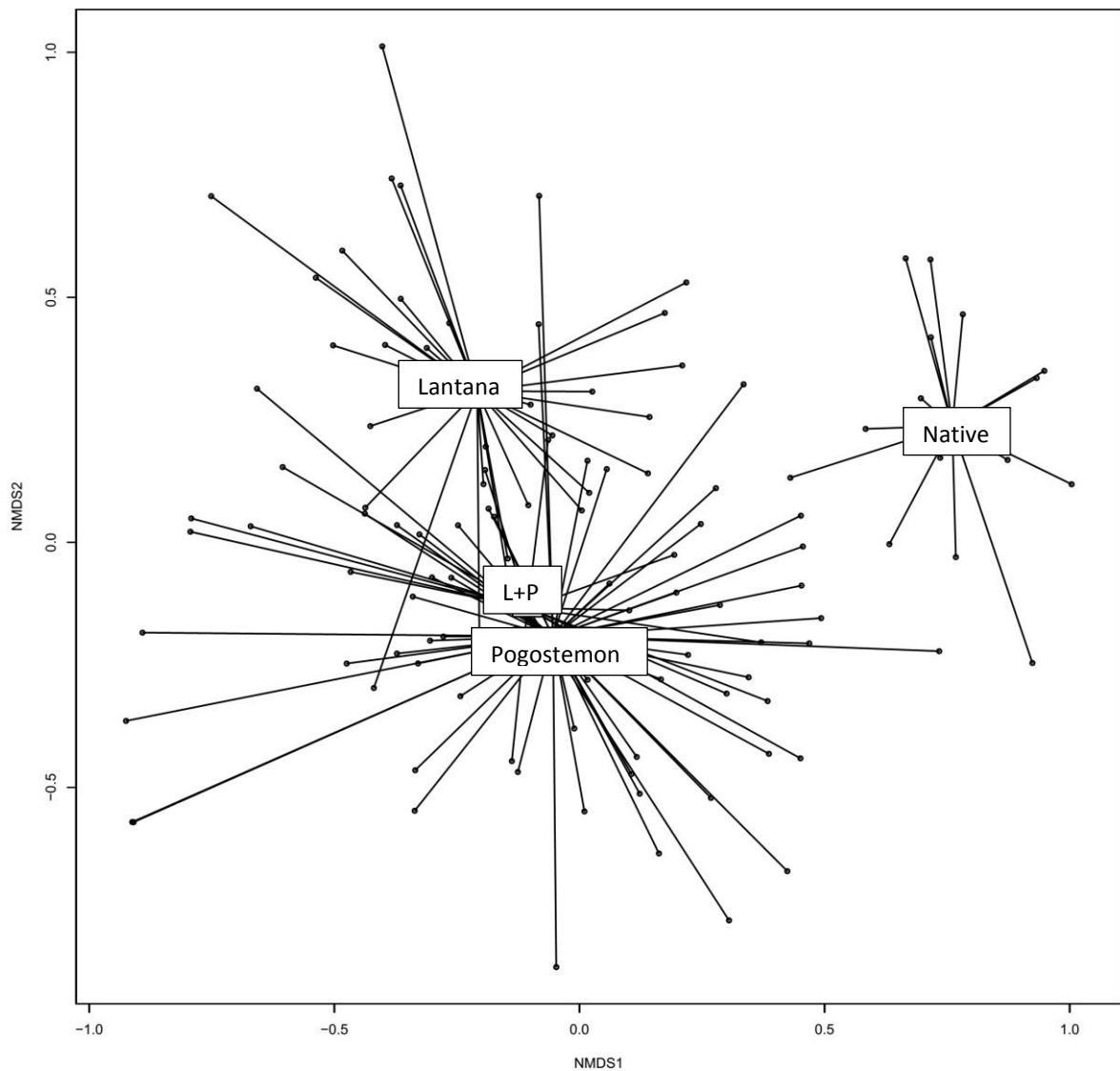


Figure 9: Plant community ordination based on the observed dissimilarities in species-sites matrix, using NMDS. Three major communities were derived which are Native (uninvaded community), Lantana, Pogostemon, however, considerable overlap was found when lantana and pogostemon occurred together (L+P).

Canonical Correspondence Analysis (CCA): Six axes were obtained by CCA for establishing correlation between native plant community (species variables) and environmental variables. Due to high prevalence of rare species in sampling plots, species which are present in twelve and/or lesser number of plots were eliminated from the analysis. Among 6 components, first four explained 87% (0.87678) of the variability (Table 6). A logical correlation was found between the plant community structure, the abundance of invasive plants and other environmental parameters used for CCA (Figure 10).

Table 6: Proportion of variations explained by different components of Canonical Correspondence Analysis (CCA) and their eigen values.

	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Eigenvalue	0.1103	0.08799	0.05013	0.0306	0.02457	0.01464
Proportion Explained	0.3467	0.27646	0.15751	0.09614	0.0772	0.04602
Cumulative Proportion	0.3467	0.62313	0.78064	0.87678	0.95398	1

34 % of the variability was explained by the first component of CCA. Soil moisture formed the major explanatory variable for component 1 (eigen value 0.1103), and accounted for moist Sal forest with high soil moisture and less significance of lantana presence (Table 7). *Colebrokia oppositifolia*, *Flemingia macrophylla*, *Syzigium cumini* were positively correlated with the axis whereas, *Mallotus phillipensis*, *Bauhinia malabarica*, *Desmodium oojeinense*, *Smilax* sp., *Casearia graveolens*, *Trema orientalis*, were found to be correlated negatively. However, a significant negative correlation was found for *Ageratum conyzoides*, which is another invasive species in India and is a native species in Central America (Appendix S7).

Component 2 (eigen value 0.08799) which explained 27 percent of the variability was dominated by abundance of Lantana and accounts for dry Sal forest with Lantana presence (Table 7). *Holarrhena antidysentrica*, was found to be positively correlated with Lantana and negative correlation was observed in *Desmodium oojeinense* and *Chloroxylon swietenia* (Appendix S7).

15 % variability was explained by Component 3 (eigen value 0.05013) which was dominated by land surface temperature of april, the axis primarily comprised of deciduous forest with significant presence of lantana and pogostemon (Table 7).

Holarrhena antidysentrica, *Schleichera oleosa*, *Colebrokia oppositifolia*, *Ageratum conyzoides*, were few of the positively correlated species, whereas, *Flemingia semialata*, *Cordia myxa*, *Shorea robusta*, *Phoenix acaulis*, *Dendrocalamus strictus* and *Asparagus racemosus* were found to be negatively correlated with the axis.

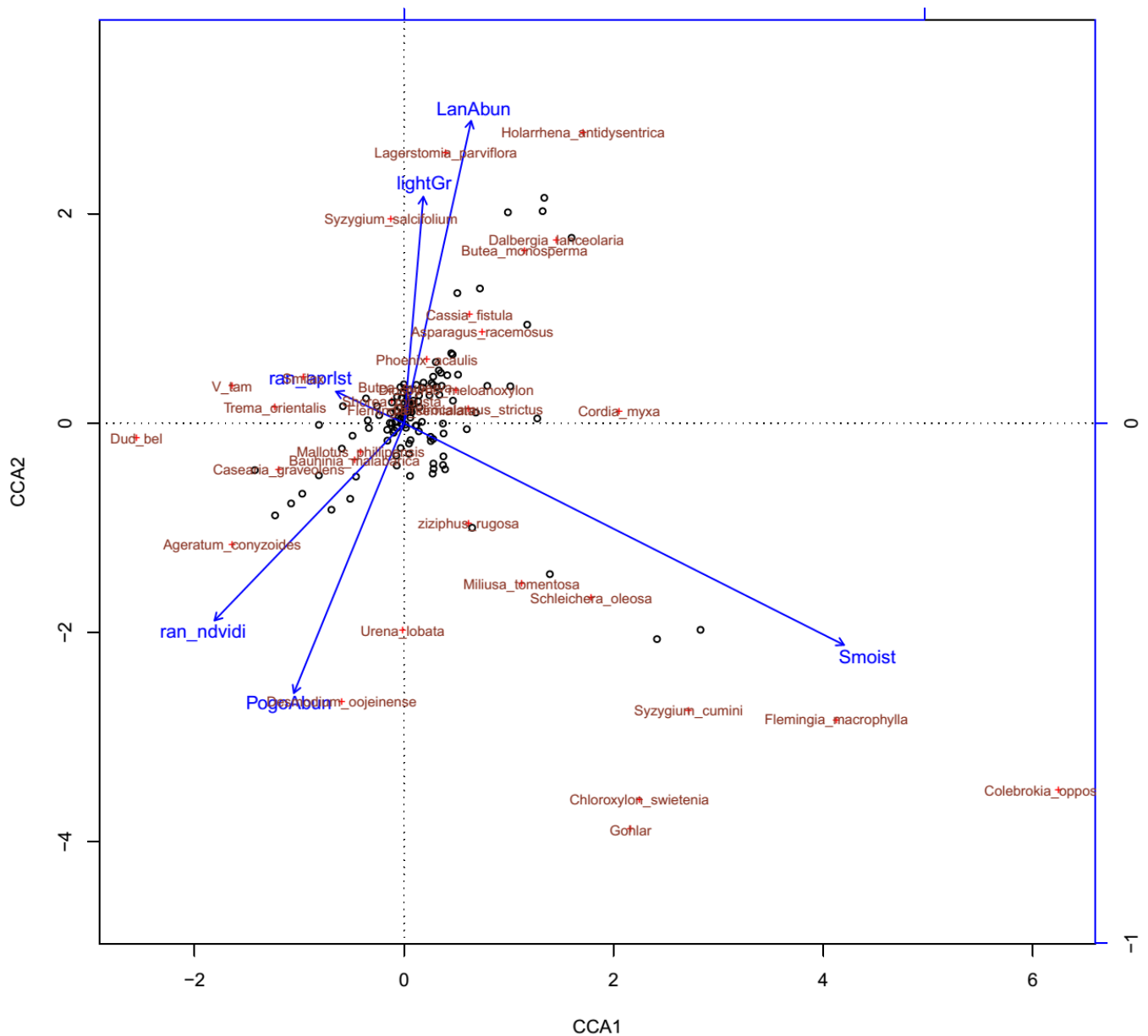


Figure 10: Correlation of Native species with abundance of lantana (LanAbun), pogostemon (PogoAbun), environmental parameters (Light intensity – lightGr, deciduousness of forest - ran_ndvidiff) and edaphic factors (soil moisture- Smoist) using Canonical Correspondence Analysis.

Component 4 and Component 5 which collectively explained 16 % of the total variability (eigen values 0.0306, 0.02457, respectively) had no presence of Lantana or Pogostemon and contained relatively moister Sal forest area (Table 7). Component 4 was interpreted to be relatively moist, cold and with high canopy cover (negative correlation of land surface temperature and light on ground), whereas component 5 accounts for significant negative correlation with lantana and pogostemon and high soil moisture. Species like *Asparagus racemosus* and *Dendrocalamus strictus* were found to be positively correlated.

Component 6 with 4 % explanation (eigen value 0.01464) had significant correlation with Pogostemon abundance and forest moistness (significant negative correlation with NDVI difference). Species like *Dendrocalamus strictus*, *Cassia fistula* and *Trema orientalis* were found to have negative correlation with the axis (Table 7).

Table 7: Relationship of environmental parameters with obtained six components of CCA. Environmental parameters like Soil moisture, lantana abundance, pogostemon abundance, light on ground, land surface temperature for the month of April, deciduousness of the forest were selected.

Environmental parameter	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Soil moisture	0.85	-0.43	0.02	-0.03	0.32	0.01
Lantana Abundance	0.13	0.58	0.12	-0.03	-0.78	-0.16
Light on ground	0.04	0.44	-0.48	-0.58	-0.47	0.15
Land surface temperature (April)	-0.13	0.06	0.54	-0.70	0.15	-0.42
Pogostemon Abundance	-0.21	-0.52	0.04	-0.25	-0.76	0.21
Forest deciduousness	-0.36	-0.38	0.04	-0.30	-0.12	-0.78

Comparing response variables along the gradient of plant invasion using linear model (ANOVA)

Effect on native plant diversity: The diversity of native plants declined significantly with lantana invasion ($p < 0.001$), pogostemon invasion ($p < 0.01$) and invasion of both species ($p < 0.05$). However the decline in diversity was more with single species

invasion (lantana=1.04, pogostemon=1.43) when compared with both the species' invasion together (1.47) (Table 8A).

Effect on native plant richness: The richness of native plants declined significantly with lantana invasion ($p < 0.001$), pogostemon invasion ($p < 0.001$) and invasion of both species ($p < 0.01$). However, the decline in richness was less with pogostemon invasion (8.92) and when both the species' invasion together (7.80) as compared to decline with lantana invasion (4.75) (Table 8B).

Effect on native rare plant richness: The richness of native rare plants declined significantly with lantana invasion ($p < 0.001$), pogostemon invasion ($p < 0.001$) and invasion of both species ($p < 0.001$). However the decline in richness was less with single species invasion (lantana= 0.50 ± 0.38 , pogostemon= 0.67 ± 0.29) when compared with both the species' invasion together (0.40 ± 0.36) (Table 8C).

Effect on native plant evenness: The evenness of native plants increased significantly with lantana invasion ($p < 0.05$), pogostemon invasion ($p < 0.05$) and insignificantly with invasion of both species ($p < 0.1$). However the increase in evenness was more with invasion of lantana (0.55) as compared to pogostemon (0.49) or both the species together (0.46) (Table 8D).

Effect on soil chemicals: Soil moisture insignificantly increased with increase in lantana cover (0.55, $p > 0.1$), significantly increased with pogostemon (0.49, $p < 0.05$) and varied insignificantly when both the species occurred together ($p > 0.1$) (Table 8E). Among soil nutrients, organic carbon increased significantly with high lantana cover (3.24, $p < 0.01$) and increasing pogostemon cover (2.46, $P < 0.01$) and varied insignificantly ($p > 0.1$) when both the species occurred together (Table 8F). Soil potassium significantly increased with high pogostemon cover (4481, $p < 0.01$) (Table 8G) and decreased with increased lantana (1736, $p < 0.05$).

Table 8: Mean values of diversity and soil parameters arranged in the categories of invasion at 10X10m scale. Different classes of no lantana (NL), low lantana (LL), medium lantana (ML), high lantana (HL), no pogostemon (NP), low pogostemon (LP), medium pogostemon (MP) and high pogostemon (HP) abundance are given. Here, Green colour denotes the highest mean value, followed by orange, yellow and red the least value. **Bold** values indicate a significant difference in the response variables as compared with the uninvaded plot (NP, NL). The estimates on errors and significance are given in Appendix S7.

A				
Shannon				
	NL	LL	ML	HL
NP	1.84	1.61	1.23	1.04
LP	1.57	1.75	1.95	1.65
MP	1.54	1.66	1.47	
HP	1.43	1.45		

B				
Richness				
	NL	LL	ML	HL
NP	17.60	7.00	5.00	4.75
LP	7.29	9.40	10.43	7.86
MP	8.71	8.67	7.80	
HP	8.92	7.70		

C				
Richness of rare species				
	NL	LL	ML	HL
NP	5.33	0.50	0.50	0.50
LP	1.29	1.30	1.43	0.57
MP	0.82	1.67	0.40	
HP	0.67	1.40		

D	Evenness			
	NL	LL	ML	HL
NP	0.38	0.63	0.59	0.55
LP	0.64	0.55	0.59	0.55
MP	0.55	0.55	0.46	
HP	0.49	0.49		

E	Soil moisture			
	NL	LL	ML	HL
NP	10.48	9.71	8.69	7.51
LP	13.11	5.95	6.81	5.62
MP	10.40	7.57	7.84	
HP	10.88	8.53		

F	Organic carbon			
	NL	LL	ML	HL
NP	1.81	1.89	1.92	3.24
LP	2.67	1.21	1.87	1.78
MP	2.46	2.11	2.46	
HP	2.46	1.71		

G	Potassium			
	NL	LL	ML	HL
NP	2955	2179	1841	1736
LP	2984	3337	3289	3504
MP	3240	2964	3478	
HP	4481	3593		

This significant decline in species richness and diversity with increase in lantana and pogostemon cover (single species invasion) indicates towards the biotic homogenization of the plant community.

CHAPTER FOUR: DISCUSSION AND CONCLUSION

The present study aimed to look at the effects of two invasive plants, a non-native invasive, *Lantana camara* complex and a native invasive, *Pogostemon benghalensis* and the difference in plant community structure with an increasing magnitude of their invasion. In addition to this, three hypotheses which are biotic homogenization hypothesis (BH), intermediate disturbance hypothesis (IDH) and invasional meltdown hypothesis (IMH) were tested (Simberloff and Von Holle 1999, Connell 1978, McKinney 1999). To test these hypotheses, the study was designed so as to control the effect of extrinsic factors like anthropogenic disturbances and establish a cause-effect relationship of altered community structure with invasive species (lantana and pogostemon).

Distribution of Invasive plants

For the first objective, the study area was extensively surveyed for the percent cover of lantana and pogostemon, which were later modelled using different Species Distribution Models (SDMs). It was found that lantana has invaded habitats that are changed by anthropogenic modifications like tourism roads, fire control lines and water bodies (Table 3). It has also invaded the edges of forest patch more as compared to the core, suggesting that fragmentation can further elevate the invasion, particularly done by anthropogenic modifications. Lantana distribution was however restricted due to remote, moist forest patches, and due to climatic heat and edaphic dry stress. Pogostemon on the other hand is best explained by moistness of forest patch, lower summer temperature and habitat opening by anthropogenic factors (Table 4). It is restricted due to climatic heat and edaphic dry stress, and remote deciduous forest (Table 4). Thus, in addition to the precise distribution map made by ensembling the correlative and mechanistic SDMs, it also provides a holistic understanding of species spatial ecology and the likely effects of any conservation management action taken by the concerned stakeholder.

In one of the most intensive survey based comparison of correlative, mechanistic and ensemble models at microscale for native and non-native invasive weedy plants I found mechanistic models and ensemble models outperformed correlative models. However, if density information from the ensemble model was removed (as it is most of the times unavailable), MaxEnt model had the best performance, but under-

predicted the species' absence. Poor performance of linear modelling (LM) and occupancy modelling (OM) amongst the correlative models can potentially be due to fitting a linear function with the most significant correlated parameter (distance from canopy openings in the present case). In areas where both the species are absent due to parameters that are less significantly correlated (temperature and moistness of the forest in present case), the former takes over the later, producing pseudo-presence and under-fitting the absences. As a result I got a higher sensitivity index but a very poor specificity index. In case of MaxEnt, it fits non-linear and interactive relations with the covariates that checks for the spatially interacting constraints (Phillips & Dudik, 2008). Hence, the specificity index of MaxEnt was highest in comparison with LM and OM.

Mechanistic BTM model on other hand considers extreme constraints that represent localized range of the species, due to which few areas within the range those are devoid of invasion may be misclassified as presence. This is resolved when density informed from intraspecific distances are incorporated to interact with the BTM. Though BDM that are produced by such interactions, need exhaustive ground survey, turned to best explain the species presence and absence. The sensitivity and specificity of BDM outnumbered any other model, so much so that the ensemble of all these models was similar to the BDM. Ensemble models with the BDM removed produced sensitivity and specificity index, which was less than either sensitivity or specificity index of other SDMs. Hence, due to intensive information on microscale densities that interact with mechanistic models, I contradict previous studies who reported poor performance of mechanistic models as compared to correlative models (e.g. Buckley et al 2010). Ensemble models based on such information not only produces a precise distribution estimate, but also provides an insight into how species are limited in the ecosystems. Particularly in case of invasive plants, such information can assist in taking adaptive decisions for invasive species management.

Species composition and community structure

For achieving the second objective, diversity parameters were derived and community ordination was carried out. Rank abundance plots obtained from the study clearly indicate the presence of more than 50 % of rare species (27 trees, 38 shrubs and 28 herbs). These species were termed 'rare' because of their occurrence in less than 10 percent of the sampled plots (<12 plots), however, this connotation of rarity is defined

for the present study and does not pertain to the rare status of the species, *per se*. These basic diagnostic graphs also provided insights about the low evenness of the study area which can be attributed to Sal forest itself, since it is one of the most homogenous forest types in the tropical India (Champion and Seth 1968).

Based on the observed dissimilarity, visual demarcation of invaded and un-invaded communities was depicted in the NMDS plot. This assessment was supported by the Kruskal stress value of 0.19, which indicates a good fit for the ordination (Figure 8). Similar results were obtained when, correlation between native plant species and independent explanatory variables like abundance of lantana and pogostemon, edaphic factors and canopy opening was established using Canonical Correspondence analysis (CCA).

In CCA, Component 1 and 2, which collectively explained 62 % of the variability in the dataset accounted for soil moisture and presence of lantana. Palatable species like *Bauhinia malabarica*, *Caseraria graveolens*, *Smilax* sp., *Schleichera oleosa*, *Miliusa tomentosa*, *Ziziphus rugosa*, *Mallotus phillipensis* were negatively loaded on these axes. This negative relationship with palatable species might indicate towards depletion of quality of forage available and facilitation of weedy species like *Colebrokia oppositifolia* which is positively correlated with the first component (Appendix S7).

With the presence of lantana and pogostemon both, negative relationship was obtained for species like *Ziziphus rugosa*, *Smilax*, *Asparagus racemosus*, *Dendrocalamus strictus*, *Phoenix acaulis*, *Shorea robusta*, *Cordia myxa* and *Flemingia semialata* on component three. *Asparagus racemosus* (Shatavar) was found to be a rare species for sal forest in the study area and is proven to have many medicinal properties (Mandal et al., 2000), depiction of a negative relationship with *Shorea* and *Asparagus* raises concern as it might indicate towards a decline in the population of the species in the longer run. Positive correlation of component three with another invasive species i.e., *Ageratum conyzoides*, supports the argument of Invasional meltdown being studied.

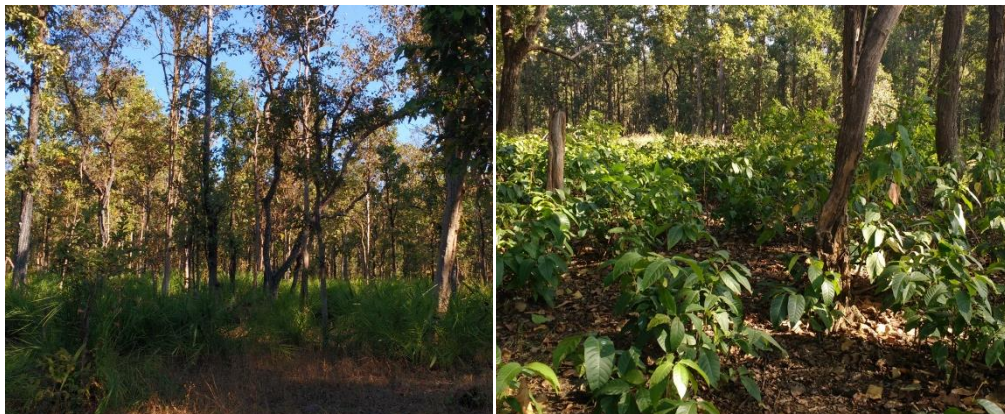
Component four and five indicated towards positive relationship obtained for above mentioned palatable and rare species. Sampling plots with dense canopies, low land surface temperature and relatively high moisture content were present in the accounted component. Negative loadings with lantana and pogostemon abundance in the

component might refer to the failure of their establishment in these forest patches. Component six of CCA, explained the presence of pogostemon and negative correlation with *Trema orientalis*, *Cassia fistula*, *Chloroxylon swietenia* and *Desmodium oojeinense* was obtained.

Biotic homogenization hypothesis

Biotic homogenization is a phenomenon where species diversity of a community declines and forms a simpler community with less number of species. In such a scenario, it is mostly few common species taking over the community assemblage and rare species are mostly eliminated. In the present study, I observed the evenness of plant assemblage to significantly increase with increase in either invasive species or when both the species occur together (in low abundance of either one or both; Table 8). Significant increase in soil organic carbon with increase in the cover of single invasive species was found. Similar to the theoretical predictions, we also observed that elevated soil organic carbon potentially elicited facilitation of selective common Fabaceae plants which in turn fixed nitrogen in the soil and facilitated lantana and pogostemon.

A significant decline in diversity and richness and a significant increase in species evenness and soil organic carbon support the notion that with increase in the abundance of invasive species, simplification of the community assemblage takes place, thus affirming the biotic homogenization hypothesis (Connell 1978).

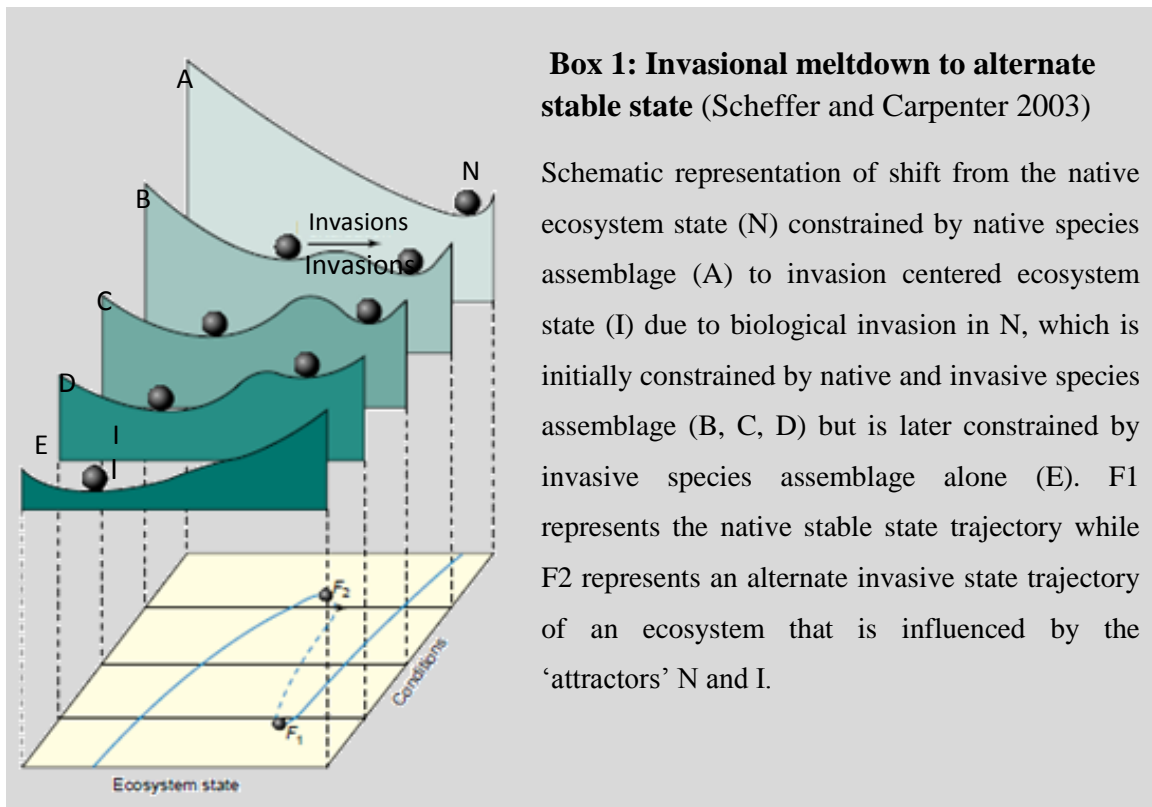


Field view 7: Sal forest area with homogenized understorey, *Phoenix acaulis* (left) and *Holarrhena antidysentrica* (right).

Invasional meltdown hypothesis

In the present study, increase in pogostemon decreased the diversity of native plants and richness of rare plants; while increase in lantana decreased the native plant diversity and rare species richness more substantially. It indicates that invasive plant species are detrimental to the native plant diversity (Fensham et al., 1994; Swarbrick et al., 1998; Batianoff and Butler, 2003; Sharma et al., 2005; Gooden et al., 2009). When both the species were present in lesser proportion (10-50% cover of the plot) there was an insignificant effect on the species diversity and richness as compared to single invasion effect. However, presence of both invasive plants in higher proportions (> 50% cover of the plot) and this combined effect might have exerted a significant and substantial decline in the native plant diversity and richness of rare species (Table 8; Appendix S7). However, decline in the native diversity or richness can only partially indicate towards invasional meltdown. As Gurevitch (2006) asserted that the invasional meltdown is not mere additive effect of two species, which also happens to be invasive, but a “*cascade of positive feedbacks that accelerates its effects like a snowball*”. In current study, I found that when both the invasive species were present, the native species diversity and richness declined, soil moisture decreased and organic carbon and potassium increased (Table 8). Invasive species are globally known to invade in potassium rich soils (Pieters & Baruch, 1997). I observed that in potassium rich soils more native (*Colebrookia oppositifolia*) and non-native (*Ageratum conyzoides*, *Achyranthus aspera*) weedy species in the plots with where pogostemon and lantana were present. This indicates towards the paradigm of facilitation of secondary invaders, but needs further validation. Hence, I observe an invasion centric assemblage as a result of invasional meltdown brought by pogostemon and lantana in the present study.

I see this Invasional meltdown as an alternate stable species assemblage to the native stable species assemblage. Where, due to perturbation caused by synergistic facilitation of invasive species the assemblage constrained by native species is shifted to the assemblage constrained by invasive species. Though in the present study, I might have unaccounted many complex interactions but, I observe a significant change in species assemblage and potential species interactions due to presence of two invasive plants. I take it a step ahead to propose that invasional meltdown can likely shift the native regime of ecological assemblage to an invasive regime (Box1).



Intermediate disturbance hypothesis:

Established negative impacts of invasive plants in the present study align with the studies on biological invasions worldwide (Catford 2012, Shea 2004). So, it is safe to assume biological invasions as a disturbance for native community. According to the intermediate disturbance hypothesis, diversity of competing species is expected to increase at intermediate frequencies of disturbance or environmental change (Connell 1978). However, in a review of more than 100 case studies, the diversity rarely peaked (<20%) due to intermediate disturbances (Mackey and Currie 2001). This can be attributed to the over-simplistic approach of IDH, it is mostly unable to inculcate, the complexity associated with the magnitude and spatial context of disturbance regimes (Chesson and Huntly, 1997). Studies that have affirmed IDH are many a times found to have skewed study design and bias in selecting ecosystems where it IDH is likely to be true (Fox 2013). In a theoretical framework, competition among the native species is weakened by disturbances and should lead towards reduced species densities. Similarly, this weakened competition should act upon all the taxa in a similar manner, or should have an enhanced effect on rare species composition and their growth rate. The difference in the growth rates between competitively superior and inferior species

determines the rates of competitive exclusion; therefore intermediate disturbances are affecting species' abundance but not coexistence.

Even in the present study, I found a linear decrease in the native plant diversity, richness and richness of rare plants (Table 8 A, B and C). When both the invasive species co-occurred at lesser densities (<50% of the plot), I observed an insignificant rise in native plant diversity, but it was still lesser when compared with the uninvaded areas. For areas, where both the plants were present in high magnitude, all the diversity and richness parameters significantly decreased. Hence, I do not see any significant peak in diversity due to intermediate invasions (single as well as multiple); rather observe a substantial decline as compared to the un-invaded community.

Sticking to the constraints of time and issue with seasonality of dataset, the study indicates towards a linear decline in diversity with increasing invasion magnitude, hence, I reject the intermediate disturbance hypothesis in the spatial context. However, community and disturbance regime are complex phenomenon and should essentially be observed over a long span of time, so, I also suggest that the patterns of community organization with respect to biological invasions should be testified over a long span of time.

With such conclusions and significant rejection power, scholars (e.g. Fox 2013) might classify present study to have accepted a sceptic hypothesis. However, I confront to the time constrain of present study, which might have potentially rejected the intermediate disturbance hypothesis, with the assumption that biological invasions can be placed in Joseph Hurd Connell's definition of 'disturbance' (e.g. Sheil and Burslem 2013).

Conclusion, personal observations and management implication:

The current study clearly points out the factors associated with invasion of *Lantana camara* and *Pogostemon benghalensis* in drier Sal forest of Kanha National Park. Lantana invasion was primarily explained by canopy openings and edges of forest and was constrained by moist forest patches, drier soil. On the other hand, pogostemon invasion was explained by canopy openings, moist forest and relatively colder forest floor. Pogostemon distribution was primarily constrained with deciduousness of forest.

With the current comparison among various species distribution models, I found that mechanistic models outperform correlative models at finer scales and ensembling

these models can not only provide better distribution maps but also informs about ecological constraints of the species.

Coming to the community organization and effect of single and multiple invasions on native plant community, I found that when lantana and pogostemon are present (either single or together) in higher abundance, it triggers change in the species composition. Being on field and taking close observations of the plant assemblage in that area, I observed an increase in common species from family Fabaceae (*Flemingia semialata*, *Cassia fistula*, etc; nitrogen fixers) with increased multiple invasions. I also observed that it was only when these two species are present together that, other native weeds (*Colebrokia oppositifolia*) and non-native (*Ageratum conyzoides*) species are present. However, it can also be an artefact of my sampling and it needs further validation.

A dramatic change in soil chemicals (increase in soil organic carbon and decrease in soil potassium) content is also found when uninvaded and twelve classes of invasion were compared. But, I would refrain myself from coming to any conclusion, since many other soil parameters like soil nitrogen, phosphorus, salinity and pH are yet to be investigated.

With the present study, it is clear that invasive species impacts the community structure and ecosystem functioning by not only the decline in diversity and richness of the native species but also modification in the abiotic components like soil nutrients.

I also found that multiple species invasion impacts richness of rare species more than single species invasion. These rare species comprise of many palatable and medicinal species like (*Asparagus racemosus*, *Buchanania lanzan*, *Phyllanthus emblica* and *Casearia graveolens*). These species are not only providing forage to various ungulates in the area, but can also indicate towards ecological health of the ecosystem.

Present study can be used as an evidence to prioritize immediate management interventions inside Sal forest. In order to shift the invasion-centric assemblage to the native species centred assemblage, consistent large scale and intensive efforts are needed to revert back the areas invaded by multiple species. Field observations pooled with the statistical outcomes suggest that intensive invasive species management is required in areas where multiple invasions are present in lesser magnitude, as the

chances of extirpation of rare species in such areas are high. In this manner, a larger area can be managed and preserved for native species.



Field view 8: Soil samples being processed on field (left) and Ninad sampling lantana invaded area (right).

References

- Araújo, M.B. and M. New, 2007. Ensemble forecasting of species distributions. *Trends in ecology & evolution*, **22**(1), pp.42-47.
- Batianoff, G.N. and D.W. Butler, 2003. Impact assessment and analysis of sixty-six priority invasive weeds in south-east Queensland. *Plant Protection Quarterly*, **18**(1), pp.11-15.
- Batten, M. Katharine, M. Kate, M. Scow, Kendi F. Davies, and Susan P. Harrison. 2006. "Two invasive plants alter soil microbial community composition in serpentine grasslands." *Biological Invasions* **8**, no. 2: 217-230).
- Blackburn, T.M., P. Pyšek, S. Bacher, J.T. Carlton, R.P. Duncan, V. Jarošík, J.R. Wilson, and D.M. Richardson, 2011. A proposed unified framework for biological invasions. *Trends in ecology & evolution*, **26**(7), pp.333-339.
- Blank, Robert R. 2008. "Biogeochemistry of plant invasion: a case study with downy brome (*Bromus tectorum*)."
*Invasive Plant Science and Management*1, no. **2**, 226-238.
- Bolker, B.M., 2008. *Ecological models and data in R*. Princeton University Press.
- Buckley, L.B., M.C., Urban, M.J. Angilletta, L.G Crozier, L.J. Rissler, and M.W. Sears, 2010. Can mechanism inform species' distribution models?. *Ecology letters*, **13**(8), pp.1041-1054.
- Cappuccino, N. and J.T. Arnason, 2006. Novel chemistry of invasive exotic plants. *Biology Letters*, **2**(2), pp.189-193.
- Catford, J.A., C.C. Daehler, H.T. Murphy, A.W. Sheppard, B.D. Hardesty, D.A. Westcott, M. Rejmánek, P.J. Bellingham, J. Pergl, C.C. Horvitz, and P.E. Hulme, 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**(3), pp.231-241.

Champion, S.H. and S.K. Seth, 1968. A revised survey of the forest types of India. A revised survey of the forest types of India.

Charles, Krebs J. 2009. "Ecology 6th Edition: The Experimental Analysis of Distribution and Abundance." Person International Edition. San Francisco, United States of America.

Chesson, P. and N. Huntly, 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, **150(5)**, pp.519-553.

Colautti, R.I., A. Ricciardi, I.A. Grigorovich, and H.J. MacIsaac, 2004. Is invasion success explained by the enemy release hypothesis?. *Ecology Letters*, **7(8)**, pp.721-733.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science*, **199(4335)**, pp.1302-1310.

Dassonville, N., S. Vanderhoeven, W. Gruber, and P. Meerts, 2007. Invasion by *Fallopia japonica* increases topsoil mineral nutrient concentrations. *Ecoscience*, **14(2)**, pp.230-240.

de Abreu, R.C. and G. Durigan, 2011. Changes in the plant community of a Brazilian grassland savannah after 22 years of invasion by *Pinus elliottii* Engelm. *Plant Ecology & Diversity*, **4(2-3)**, pp.269-278.

Ehrenfeld, J.G., 2009. Implications of Invasive Species for Belowground Community and Nutrient Processes1.

Ehrenfeld, J.G., P. Kourtev, and W. Huang, 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological applications*, **11(5)**, pp.1287-1300.

Elith, J., M. Kearney, and S. Phillips, 2010. The art of modelling range-shifting species. *Methods in ecology and evolution*, **1(4)**, pp.330-342.

Elton, Charles S., 1958. "The ecology of invasions by plants and animals." Methuen, London 18.

Ens, E.J., J.B. Bremner, K. French, and J. Korth, 2009. Identification of volatile compounds released by roots of an invasive plant, bitou bush

Chrysanthemoides monilifera spp. rotundata), and their inhibition of native seedling growth. *Biological invasions*, **11(2)**, pp.275-287.

Ens, E.J., K. French, and J.B. Bremner, 2009. Evidence for allelopathy as a mechanism of community composition change by an invasive exotic shrub, *Chrysanthemoides monilifera* spp. rotundata. *Plant and Soil*, **316(1-2)**, pp.125-137.

Entekhabi, D., E.G. Njoku, P.E. O'Neill, K.H. Kellogg, W.T. Crow, W.N. Edelstein, J.K. Entin, S.D. Goodman, T.J. Jackson, J. Johnson, and J. Kimball, 2010. The soil moisture active passive (SMAP) mission. *Proceedings of the IEEE*, **98(5)**, pp.704-716.

Entekhabi, D., E.G. Njoku, P.E. O'Neill, K.H., Kellogg, W.T. Crow, W.N. Edelstein, J.K. Entin, S.D. Goodman, T.J. Jackson, J. Johnson, and J. Kimball, 2010. The soil moisture active passive (SMAP) mission. *Proceedings of the IEEE*, **98(5)**, pp.704-716.

Fensham, R.J., R.J. Fairfax, and R.J. Cannell, 1994. The invasion of *Lantana camara* L. in forty mile scrub National Park, north Queensland. *Austral Ecology*, **19(3)**, pp.297-305.

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*.

Fox, J.W., 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in ecology & evolution*, **28(2)**, pp.86-92.

Gioria, M. and B.A. Osborne, 2014. Resource competition in plant invasions: emerging patterns and research needs. *Frontiers in plant science*, **5**, p.501.

Gioria, M., B. Dieterich, and B. Osborne, 2011, December. Battle of the giants: primary and secondary invasions by large herbaceous species. In *Biology and Environment: Proceedings of the Royal Irish Academy* (pp. 177-193). Royal Irish Academy.

Gooden, B., K. French, P.J. Turner, and P.O. Downey, 2009. Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biological conservation*, **142(11)**, pp.2631-2641.

Green, P.T., D.J. O'Dowd, K.L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nally, 2011. Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecology*, **92(9)**, pp.1758-1768.

Guisan, A., S.B. Weiss, and A.D. Weiss, 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecology*, **143(1)**, pp.107-122.

Gurevitch, J., S.M. Scheiner, and G.A. Fox, 2006. The ecology of plants (pp. 215-216).

Hanway, J.J. and H. Heidel, 1952. Soil analysis methods as used in Iowa state college soil testing laboratory. *Iowa agric*, **57**, pp.1-31.

Hejda, M., P. Pyšek, and V. Jarošík, 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97(3)**, pp.393-403.

Hines, J.E., 2006. PRESENCE 2: Software to estimate patch occupancy and related parameters. USGS-PWRC.

Hosmer, D.W. and S. Lemeshow, 1989. *Applied regression analysis*. New York, John Willey.

Hughes, F., P.M. Vitousek, and T. Tunison, 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology*, **72(2)**, pp.743-747.

Jhala, Y.V, Q, Qureshi and R, Gopal, 2015. Monitoring tigers, co-predators and prey in India.

Johnson, J.B. and K.S. Omland, 2004. Model selection in ecology and evolution. *Trends in ecology & evolution*, **19(2)**, pp.101-108.

Keane, R.M. and M.J. Crawley, 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17(4)**, pp.164-170.

Kindt, R. and M.R. Kindt, 2016. Package 'BiodiversityR'.

- Krishen, P. 2013. Jungle trees of Central India.
- Krivoruchko, K., 2012. Empirical bayesian kriging. ESRI: Redlands, CA, USA.
- MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J. Andrew Royle, and C.A. Langtimm, 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83(8)**, pp.2248-2255.
- Mackey, R.L. and D.J. Currie, 2001. The diversity–disturbance relationship: is it generally strong and peaked?. *Ecology*, **82(12)**, pp.3479-3492.
- Mandal, S.C., A. Nandy, M. Pal, and B.P. Saha, 2000. Evaluation of antibacterial activity of *Asparagus racemosus* Willd. root. *Phytotherapy Research*, **14(2)**, pp.118-119.
- Manel, S., H.C. Williams, and S.J. Ormerod, 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of applied Ecology*, **38(5)**, pp.921-931.
- Martin, R. Melissa W. Philip 2008. Tipping, and James O. Sickman. "Invasion by an exotic tree alters above and belowground ecosystem components." *Biological invasions*, **8** 1883-1894.
- McGrath, D.A. and M.A. Binkley, 2009. *Microstegium vimineum* invasion changes soil chemistry and microarthropod communities in Cumberland Plateau forests. *Southeastern Naturalist*, **8(1)**, pp.141-156.
- McKinney, M.L. and J.L. Lockwood, 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in ecology & evolution*, **14(11)**, pp.450-453.
- Mu, Q., Zhao, M. and Running, S.W., 2013. MODIS Global Terrestrial Evapotranspiration (ET) Product (NASA MOD16A2/A3). Algorithm Theoretical Basis Document, Collection, 5.
- Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, H. Wagner, and M.J. Oksanen, 2013. Package ‘vegan’. *Community ecology package*, version, **2(9)**.

Phillips, S.J. and M. Dudík, 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31(2)**, pp.161-175.

Pieters, A. and Z. Baruch, 1997. Soil depth and fertility effects on biomass and nutrient allocation in jaraguagrass. *Journal of Range Management*, pp.268-273.

Pyšek, P., V. Jarošík, P.E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vilà, 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18(5)**, pp.1725-1737.

Ray, A. and S. Quader, 2014. Genetic diversity and population structure of *Lantana camara* in India indicates multiple introductions and gene flow. *Plant Biology*, **16(3)**, pp.651-658.

Ray, A. and Ray, R., 2014. Rapid divergence of ecotypes of an invasive plant. *AoB Plants*, **6**, p.plu052.

Richards, C.L., O. Bossdorf, N.Z. Muth, J. Gurevitch, and M. Pigliucci, 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology letters*, **9(8)**, pp.981-993.

Roy, D.P., V. Kovalsky, H.K. Zhang, E.F. Vermote, L. Yan, S.S. Kumar, and A. Egorov, 2016. Characterization of Landsat-7 to Landsat-8 reflective wavelength and normalized difference vegetation index continuity. *Remote Sensing of Environment*, **185**, pp.57-70.

Rozenstein, O., Z. Qin, Y. Derimian, and A. Karnieli, 2014. Derivation of land surface temperature for Landsat-8 TIRS using a split window algorithm. *Sensors*, **14(4)**, pp.5768-5780.

Sardans, J. and J. Peñuelas, 2015. Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography*, **24(3)**, pp.261-275.

Sax, D.F., J.J. Stachowicz, and S.D. Gaines, 2005. Species invasions: insights into ecology, evolution and biogeography.

Sharma, G.P. and A.S. Raghubanshi, 2009. Lantana invasion alters soil nitrogen pools and processes in the tropical dry deciduous forest of India. *Applied Soil Ecology*, **42(2)**, pp.134-140.

Sharma, G.P., A.S. Raghubanshi, and J.S. Singh, 2005. Lantana invasion: an overview. *Weed Biology and Management*, **5(4)**, pp.157-165.

Shea, K., S.H. Roxburgh, and E.S. Rauschert, 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology letters*, **7(6)**, pp.491-508.

Shea, Katriona, and P. Chesson, 2002. "Community ecology theory as a framework for biological invasions." *Trends in Ecology & Evolution* **17**, no. 4 170-176.

Sheil, D. and D.F.R.P. Burslem, 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. *Trends Ecol Evol*, **28**, pp.571-572.

Simberloff, D. and B. Von Holle, 1999. Positive interactions of nonindigenous species: invasional meltdown?. *Biological invasions*, **1(1)**, pp.21-32.

Simberloff, D., 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both?. *Ecology Letters*, **9(8)**, pp.912-919.

Swarbrick, J.T., B.W. Willson, M.A. Hannan-Jones, 1998. *Lantana camara* L., in: F. D. Panetta, R. H. Groves, and R. C. H. Shephard, (Eds.), *The Biology of Australian Weeds*. RG and FJ Richardson, Melbourne, pp. 119-140.

Team, R.C., 2014. *R: A language and environment for statistical computing (Version 3.0. 2)*. R Foundation for Statistical Computing, Vienna, Austria.

Ter Braak, C.J., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. In *Theory and models in vegetation science* (pp. 69-77).

Thelen, G.C., J.M. Vivanco, B. Newingham, W. Good, H.P. Bais, P. Landres, A. Caesar, and R.M. Callaway, 2005. Insect herbivory stimulates allelopathic exudation by an invasive plant and the suppression of natives. *Ecology Letters*, **8(2)**, pp.209-217.

Walkley, A. and I.A. Black, 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil science*, **37(1)**, pp.29-38.

Werts, C.E. and R.L. Linn, 1970. A general linear model for studying growth. *Psychological Bulletin*, **73(1)**, p.17.

Wijayabandara, S.M.K.H., K.M.G.G. Jayasuriya, and J.L.D.H.C Jayasinghe, 2013. Seed dormancy, storage behavior and germination of an exotic invasive species, *Lantana camara* L.(Verbenaceae). *International Research Journal of Biological Sciences*, **2(1)**, pp.7-14.

Wilkinson, D.M., 1999. The disturbing history of intermediate disturbance. *Oikos*, pp.145-147.

Wyckoff, P.H., A. Shaffer, B. Hucka, M. Bombyk, and A. Wipf, 2014. No evidence of facilitation between invasive *Rhamnus cathartica* (European buckthorn) and invasive earthworms in west central Minnesota. *Pedobiologia*, **57(4)**, pp.311-317.

Zar, J.H., 1999. *Biostatistical analysis*. Pearson Education India.

<http://www.bbcearth.com/modal/episode-one/>

<http://www.cabi.org/>



Appendix S1 : Datasheet for sampling Trees and Shrubs (including other invasive species like Hyptis and Ageratum, and highly abundant grasses, If any.)

GPS Latitude (N)	GPS Longitude (E)	Lan%	Pogo%	Oth.Inv.	Soil Temp.	Range	Terrain		Ground Substrate	Observer
A	A						Flat		Sand	
B	B					Beat	Gentle slope		Silt	Date
C	C						Moderate slope		Loam	
D	D					Camp	Steep		Clay	Time
E	E						Undulating/Rugged		Rocky/Gravelly	

ID	Trees (in 10m x 10m)						Shrubs (in 10m x 10m)					
	Species	Number	Phenology	Canopy	GBH	height	Species	Number	Phenology	Height	Canopy	

**Tree & Shrub Phenology codes: 1) no leaves (bare branches), 2) no leaves plus flowers 3) no leaves plus fruit, & flower, 4) leaf bud burst, 5) green leaves 6) green leaves + flower, 7) green leaves plus fruit (& flower), 8) brown leaves or burnt.
If in more than one phase, e.g. some in leaf & others in flower, mention "%" in each phenological phase, like 90% leaf and 10% flower.*

Appendix S2: Datasheet for sampling Ground cover.

Recorder..... Date..... Time..... Field staff.....

Beat:

Plot:

P L O T	Litter				grass					herbs					Bare ground%	Light ground			
	% cover	Dry %	Wet %	Dept h-cm	Dry %	Green %	Sp (abundance)					% cover	Sp (abundance + phenology)						
							1	2	3	4	5		1	2			3	4	5
A	a																		
	b																		
	c																		
B	a																		
	b																		
	c																		
C	a																		
	b																		
	c																		
D	a																		
	b																		
	c																		
E	a																		
	b																		
	c																		

Comments:

Appendix S3: Information on scale and source of remotely sensed data used for present study

Dataset	Scale and pre-processing	Source
Worldclim data representing Temperature and Rainfall parameters	1 km (rescale to 100m by PRISM)	Hijman 2017
Pre-monsoon and Post-monsoon NDVI	30 m (Derived from the near infrared and infrared bands of Landsat 8 for year 2016-2017)	Roy 2014
Soil Surface Temperature	100m (Derived from the thermal bands of Landsat 8 for year 2016-2017)	Rozenstein 2014
Evapotranspiration rate	1 km	Mu 2013
Soil Moisture Active Passive	250m	Entekhabi 2010
Tourism road, Water streams, Forest type map	30m	Kanha Management Plan 2010

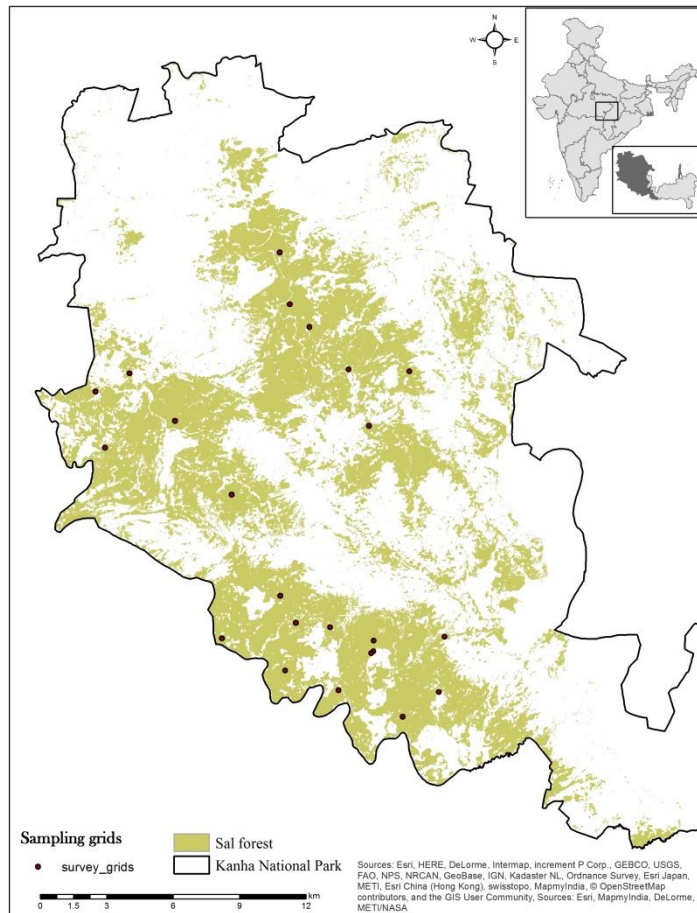
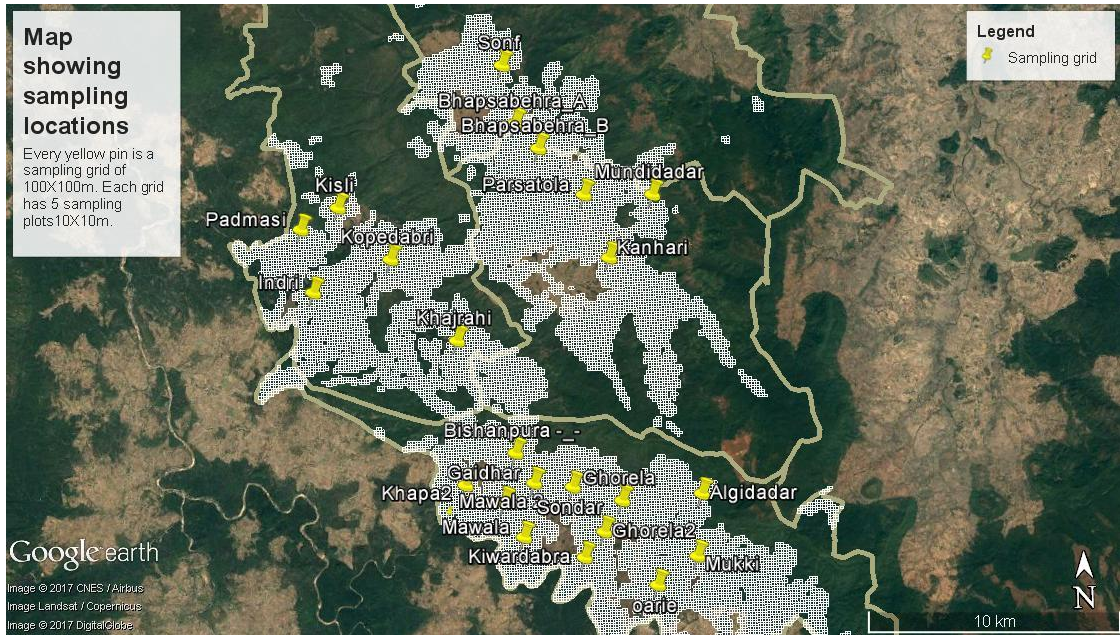


Figure 11: Map showing the location of 24 grids (100X100m).

Appendix S4

Lantana occupancy model selection

Model	AIC	delta AIC
~Lantana presence ~ Distance from canopy openings + Distance from edge + Summer temperature + Post-monsoon NDVI + Moistness of forest + Annual temperature	5412.383	0
~Lantana presence ~ Post-monsoon NDVI	5554.35	141.9679
~Lantana presence ~ Moistness of forest	5554.35	141.9679
~Lantana presence ~ Distance from edge + Distance from canopy openings + Summer temperature	5743.375	330.9928
~Lantana presence ~ Distance from canopy openings	5746.974	334.5919
~Lantana presence ~ Annual temperature	5813.334	400.9519
~Lantana presence ~ Distance from edge	5819.299	406.9164
~Lantana presence ~ Summer temperature	5819.743	407.3606
~Lantana presence~ Null Model	5822.37	409.9873

Pogostemon occupancy model selection

MODEL	AIC	delta AIC
~Pogostemon presence ~ Summer temperature + Distance from edge + Distance from canopy openings + Post-monsoon NDVI + Moistness of forest	5308.732	0
~Pogostemon presence ~ Post-monsoon NDVI	5716.492	407.7606
~Pogostemon presence ~ Moistness of forest	5716.492	407.7606
~Pogostemon presence ~ Distance from edge + Distance from canopy openings + Summer temperature	5753.535	444.803
~Pogostemon presence ~ Summer temperature	5896.788	588.0561
~Pogostemon presence ~ Distance from canopy openings	5944.769	636.0374
~Pogostemon presence ~ Null model	6035.636	726.9046
~Pogostemon presence ~ Distance from edge	6037.437	728.7048
~Pogostemon presence ~ Annual temperature	6037.473	728.7416

Appendix S5: Rank abundance plots for tree, shrub and herb species in the study area

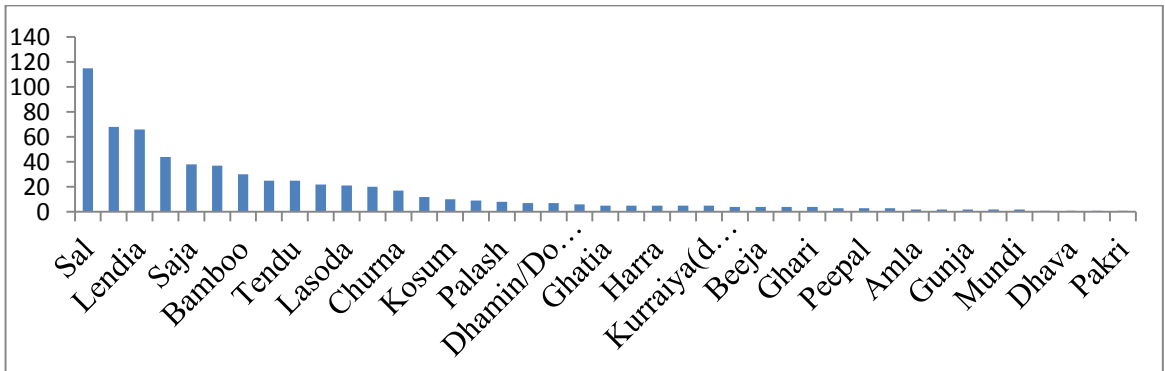


Figure a: Rank abundance plot for trees.

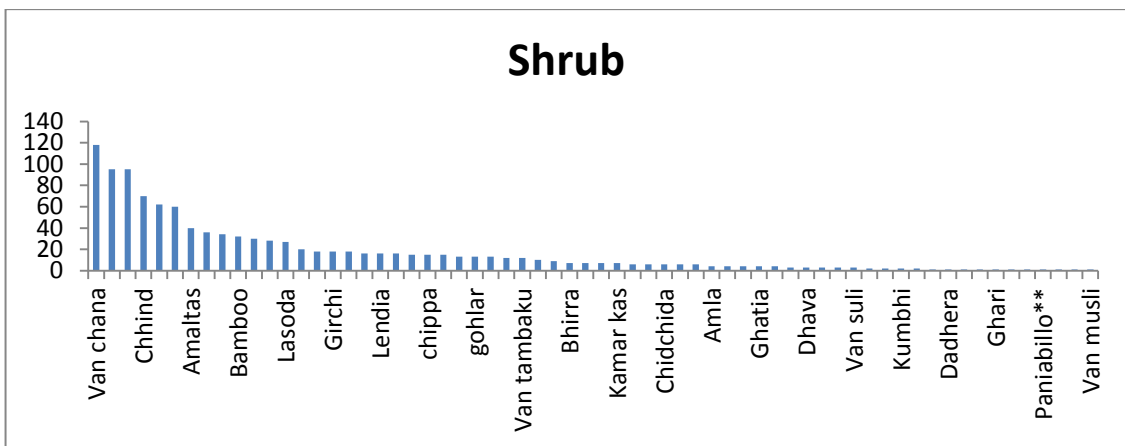


Figure b: Rank abundance plot for shrubs.

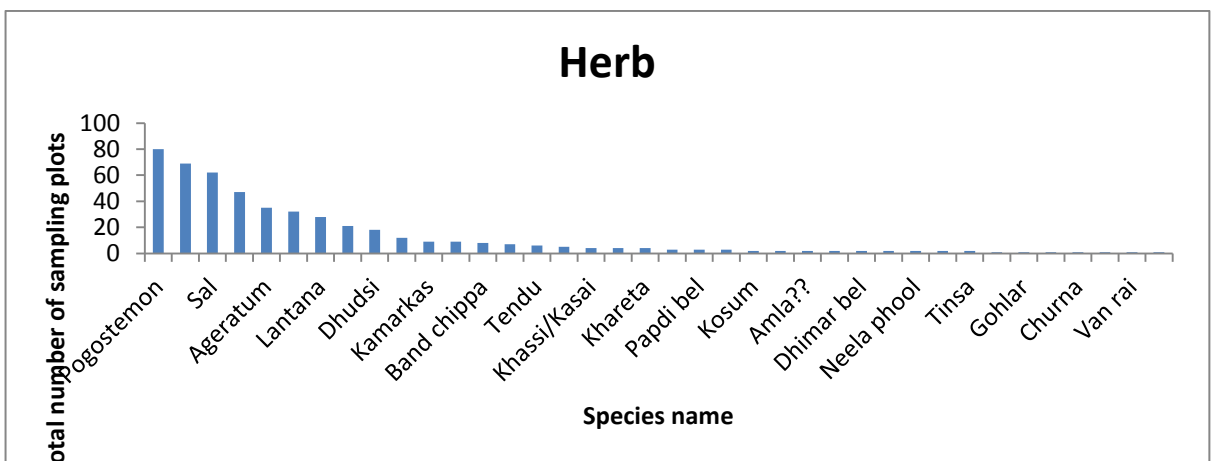


Figure c: Rank abundance plot for herbs.

Appendix S6: Loadings of various components of CCA on individual species.

Species	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Ageratum_conyzoides	-0.95	-0.64	0.83	-0.24	0.14	-0.21
Asparagus_racemosus	0.43	0.47	-0.89	0.08	1.49	1.06
Bauhinia_malabarica	-0.27	-0.20	0.27	-0.58	0.29	-0.35
Butea_monosperma	0.66	0.89	0.32	-0.38	1.21	0.17
Butea_superva	0.01	0.18	0.66	0.12	-0.12	0.65
Casearia_graveolens	-0.69	-0.25	0.34	-1.02	0.33	1.20
Cassia_fistula	0.36	0.56	0.06	0.20	-0.40	-1.34
Chloroxylon_swietenia	1.29	-1.97	0.13	-1.42	0.08	-0.72
Colebrokia_oppositifolia	3.60	-1.92	0.96	-0.12	-0.14	-0.28
Cordia_myxa	1.18	0.06	-0.11	-0.64	1.01	1.38
Dalbergia_lanceolaria	0.84	0.95	0.13	-1.17	-1.32	0.33
Dendrocalamus_strictus	0.35	0.07	-0.69	0.27	1.19	-0.98
Desmodium_oojeinense	-0.34	-1.45	0.39	-0.26	0.34	-0.47
Diospyros_meloanoxylon	0.29	0.16	0.00	-0.50	-0.36	0.44
Dud_bel	-1.47	-0.09	0.50	2.69	0.56	1.14
Flemingia_macrophylla	2.38	-1.55	0.74	0.27	0.73	-0.36
Flemingia_semialata	0.04	0.06	-0.06	-0.09	-0.34	0.00
Gohlar	1.25	-2.12	-1.60	1.75	-0.44	0.14
Holarrhena_antidysentrica	0.99	1.50	1.21	0.33	0.20	-0.08
Kamar kas	-0.07	1.06	-1.72	0.86	0.13	-1.27
Lagerstomia_parviflora	0.23	1.40	-0.04	-0.33	-0.09	0.65
Mallotus_phillipensis	-0.24	-0.16	0.13	0.64	-0.43	0.12
Miliusa_tomentosa	0.65	-0.84	0.09	0.35	0.22	-0.02
Phoenix_acaulis	0.13	0.33	-0.44	0.28	-0.21	0.07
Schleichera_oleosa	1.03	-0.92	0.98	0.74	0.64	0.70
Shorea_robusta	-0.07	0.11	-0.30	-0.25	0.18	0.06
Smilax	-0.55	0.23	-0.92	-0.04	1.12	1.20
Syzygium_cumini	1.57	-1.50	0.13	-0.24	-0.05	0.35
Trema_orientalis	-0.71	0.08	0.50	0.79	-0.17	-1.60
Urena_lobata	-0.01	-1.09	0.05	-0.04	0.25	-0.28
V_tam	-0.95	0.19	0.05	0.44	0.69	-0.01
ziziphus_rugosa	0.36	-0.53	-1.08	1.09	0.82	1.08

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.1 : Evaluating differences in mean values of Shannon-weaver diversity among thirteen invasion categories using Linear Model. For common species richness and richness of rare species, the data was log transformed ($\ln(\text{rich}+1)$).

Shannon				
	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	1.84086	0.08881	< 2e-16	***
HPLL	-0.4439	0.14043	0.00205	**
HPNL	-0.415	0.13322	0.00236	**
LPHL	-0.1954	0.12783	0.12923	
LPLL	-0.0948	0.14043	0.5011	
LPML	0.11051	0.15745	0.4843	
LPNL	-0.2699	0.12185	0.02886	*
MPLL	-0.1786	0.21755	0.4134	
MPML	-0.3677	0.17763	0.04085	*
MPNL	-0.3027	0.12185	0.01455	*
NPHL	-0.8037	0.19357	6.64E-05	***
NPLL	-0.2358	0.19357	0.22587	
NPML	-0.6146	0.25894	0.0194	*

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.2: Evaluating differences in mean values of native species' richness among thirteen invasion categories using Linear Model.

	Richness			
	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	2.8299	0.1025	< 2e-16	***
HPLL	-0.6332	0.1621	0.00016	***
HPNL	-0.6434	0.1537	5.87E-05	***
LPHL	-0.5643	0.1475	0.00022	***
LPLL	-0.4535	0.1621	0.0061	**
LPML	-0.3261	0.1817	0.0755	.
LPNL	-0.7928	0.1406	1.42E-07	***
MPLL	-0.5587	0.2511	0.02815	*
MPML	-0.576	0.205	0.0059	**
MPNL	-0.6619	0.1406	7.56E-06	***
NPHL	-1.1304	0.2234	1.75E-06	***
NPLL	-0.7544	0.2234	0.00102	**
NPML	-1.0522	0.2988	0.00063	***

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.3: Evaluating differences in mean values of rare species' richness among thirteen invasion categories using Linear Model.

Richness of rare species				
	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	1.7744	0.1309	< 2e-16	***
HPLL	-1.0353	0.2069	2.22E-06	***
HPNL	-1.3602	0.1963	3.29E-10	***
LPHL	-1.3988	0.1883	2.83E-11	***
LPLL	-1.0407	0.2069	1.99E-06	***
LPML	-1.0065	0.232	3.26E-05	***
LPNL	-1.1558	0.1795	3.51E-09	***
MPLL	-0.946	0.3205	0.00389	**
MPML	-1.4971	0.2617	9.75E-08	***
MPNL	-1.3396	0.1795	2.38E-11	***
NPHL	-1.4278	0.2852	2.19E-06	***
NPLL	-1.7744	0.2852	9.75E-09	***
NPML	-1.4278	0.3815	0.0003	***

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.4: Evaluating differences in mean values of soil moisture content among thirteen invasion categories using Linear Model.

Soil Moisture				
Smoist	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	10.4847	0.95908	$< 2e-16$	***
HPLL	-1.9566	1.51643	0.19974	
HPNL	0.39252	1.43861	0.7855	
LPHL	-4.8667	1.38035	0.00062	***
LPLL	-4.5362	1.51643	0.00345	**
LPML	-3.6735	1.70026	0.03296	*
LPNL	2.6243	1.31584	0.04865	*
MPLL	-2.9122	2.34925	0.21783	
MPML	-2.6427	1.91815	0.17116	
MPNL	-0.0879	1.31584	0.94688	
NPHL	-2.979	2.09026	0.15701	
NPLL	-0.7735	2.09026	0.71208	
NPML	-1.7919	2.79616	0.52299	

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.5: Evaluating differences in mean values of soil potassium (mg/kg) among thirteen invasion categories using Linear Model.

K	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	2954.56	334.452	2.20E-14	***
HPLL	638.484	528.815	0.22995	
HPNL	1526.22	501.678	0.00295	**
LPHL	549.875	481.359	0.25586	
LPLL	382.304	528.815	0.47129	
LPML	334.853	592.92	0.57342	
LPNL	29.066	458.864	0.94961	
MPLL	9.644	819.237	0.99063	
MPML	522.967	668.904	0.43604	
MPNL	285.259	458.864	0.53549	
NPHL	-1218.9	728.921	0.0974	.
NPLL	-775.74	728.921	0.28962	
NPML	-1113.4	975.087	0.25606	

Appendix S7: Results of Linear Model analysis (ANOVA framework).

Table 7.6: Evaluating differences in mean values of soil organic carbon (%) among thirteen invasion categories using Linear Model.

OC	Estimate	Std. Error	Pr(> t)	
NPNL(uninvaded)	1.80914	0.19702	3.61E-15	***
HPLL	-0.1029	0.31151	0.74175	
HPNL	0.65394	0.29553	0.02904	*
LPHL	-0.0309	0.28356	0.91336	
LPLL	-0.5957	0.31151	0.05852	.
LPML	0.05713	0.34928	0.87039	
LPNL	0.86288	0.27031	0.00185	**
MPLL	0.30352	0.4826	0.53073	
MPML	0.64722	0.39404	0.10342	
MPNL	0.64872	0.27031	0.01813	*
NPHL	1.43477	0.42939	0.00115	**
NPLL	0.08052	0.42939	0.8516	
NPML	0.10756	0.5744	0.85182	

Appendix S8: List of shrubs recorded during field work.

SHRUB			
Vernacular name	Scientific name	Vernacular name	Scientific name
Ageratum	<i>Ageratum conyzoides</i>	Gud sukri	<i>Trema orientalis</i>
Amaltas	<i>Cassia fistula</i>	Jamun	<i>Syzygium cumini</i>
Amla	<i>Embelica officinalis</i>	Katjamun	<i>Syzygium salcifolium</i>
Amti	<i>Bauhinia malabarica</i>	Kakai kata	<i>Bridelia retusa</i>
Bamboo	<i>Dendrocalamus strictus</i>	Kamar kas	
Band chippa	<i>Flemingia macrophylla</i>	Kari	<i>Miliusa tomentosa</i>
Barga	<i>Kydia calycina</i>	Kasai/Khassi	<i>Bridelia retusa</i>
Beeja	<i>Pterocarpus marsupium</i>	Katori	<i>Radermachera xylocarpa</i>
Bhador	<i>Butea superva</i>	kosum	<i>Schleichera oleosa</i>
Bhirra	<i>Chloroxylon swietenia</i>	Kumbhi	<i>Careya arborea</i>
Char	<i>Buchnanania lanzan</i>	Lantana	<i>Lantana camara</i>
Chhind	<i>Phoenix acaulis</i>	Lasoda	<i>Cordia myxa</i>
Chidchida	<i>Acairanthus aspera</i>	Lendia	<i>Lagerstomia parviflora</i>
chippa	<i>Urena lobata</i>	Mainhar	<i>Catunaregam spinosa</i>
Churna	<i>ziziphus rugosa</i>	Mohin bela	<i>Bauhinia vahlii</i>
chutni plant	<i>Antidesma acidum</i>	Mohti	<i>Colebrokia oppositifolia</i>
Dadhera	<i>Bauhinia racemosa</i>	Palash	<i>Butea monosperma</i>
Dhamin	<i>Grewia eriocarpa</i>	Paniabillo	<i>Gardenia latifolia</i>
Dhandhani		Papdi	<i>Pavetta crassicaulis</i>
Dhava	<i>Anogeissus latifolia</i>	Patavan	<i>Diospyros montana</i>
Dhimar	<i>chnocarpus frutescens</i>	Pogostemon	<i>Pogostemon bengalhensis</i>
Dhoban	<i>Dalbergia lanceolaria</i>	Ram datun	<i>Smilax</i>
Dodhe bel		Saja	<i>Terminalia elliptica</i>
Dudhi	<i>Holarrhena antidysentrica</i>	Sal	<i>Shorea robusta</i>
dudhi bel		Sendur	<i>Mallotus phillipensis</i>
Dudhi2	<i>Writia tinctoria</i>	Shatavar	<i>Asparagus racemosus</i>
Ghari	<i>Lannea coromandelica</i>	Tendu	<i>Diospyros meloanoxylon</i>
Ghatia	<i>Ziziphus xylopyrus</i>	Tinsa	<i>Desmodium oojeinense</i>
Girchi	<i>Casearia graveolens</i>	Van chana	<i>Flemingia semialata</i>

Appendix S9: List of trees recorded during field work.

TREE			
Vernacular name	Scientific name	Vernacular name	Scientific name
Amaltas	<i>Cassia fistula</i>	Kari	<i>Miliusa tomentosa</i>
Amla	<i>Phyllanthus emblica</i>	Kasai/Khassi	<i>Bridelia retusa</i>
Amti	<i>Bauhinia malabarica</i>	Katori	<i>Radermachera xylocarpa</i>
Bamboo	<i>Dendrocalamus strictus</i>	Khamer	<i>Gmelina arborea</i>
Barga	<i>Kydia calycina</i>	Kosum	<i>Schleichera oleosa</i>
Beeja	<i>Pterocarpus marsupium</i>	Kumbhi	<i>Careya arborea</i>
			<i>Holarrhena</i>
Bhilva	<i>Semecarpus anacardium</i>	Kurraiya(dudhi)	<i>antidysentrica</i>
Bhirra	<i>Chloroxylon swietenia</i>	Lasoda	<i>Cordia myxa</i>
Bhormal	<i>Hymenodictyon orixense</i>	Lendia	<i>Lagerstroemia parviflora</i>
Char	<i>Buchnanania lanzan</i>	Mahua	<i>Madhuca latifolia</i>
Churna	<i>Ziziphus rugosa</i>	Mohan bela	<i>Bauhinia vahlii</i>
Dadhera	<i>Bauhinia racemosa</i>	Mundi	<i>Mitragyna parviflora</i>
Dhamin/Dohan	<i>Grewia eriocarpa</i>	Pakri	<i>Ficus cupulata</i>
Dhava	<i>Anogeissus latifolia</i>	Palash	<i>Butea monosperma</i>
Dhoban	<i>Dalbergia lanceolaria</i>	Peepal	<i>Ficus religiosa</i>
Ghari	<i>Lannea coromandelica</i>	Saja	<i>Terminalia elliptica</i>
Ghari	<i>Lannea coromandelica</i>	Sal	<i>Shorea robusta</i>
Ghatia	<i>zizyphus xylopyrus</i>	Sendur	<i>Mallotus philippensis</i>
Haldu	<i>Haldina cordifolia</i>	Tendu	<i>Diospyros melanoxylon</i>
Harra	<i>Terminalia chebula</i>	Thod	<i>Bauhinia roxburghiana</i>
Jamun	<i>Syzigium cumini</i>	Tinsa	<i>Desmodium oojeinense</i>

Appendix S10: List of herbs recorded during field work.

HERB			
Vernacular name	Scientific name	Vernacular name	Scientific name
Ageratum	<i>Ageratum conyzoides</i>	Jamun	<i>Syzigium cumini</i>
Amla	<i>Phyllanthus emblica</i>	Kamarkas	
Amti	<i>Bauhinia malabarica</i>	Khareta	
Band chippa	<i>Flemingia macrophylla</i>	Khassi/Kasai	<i>Bridelia retusa</i>
Beeja	<i>Pterocarpus marsupium</i>	Kosum	<i>Schleichera oleosa</i>
Chidchida	<i>Acairanthus aspera</i>	Lantana	<i>Lantana camara</i>
Churna	<i>Ziziphus rugosa</i>	Neela phool	
Dhimar bel		Papdi bel	
Dhoban	<i>Dalbergia lanceolaria</i>	Pogostemon	<i>Pogostemon bengalhensis</i>
Dhudsi		Ram datun	<i>Smilax</i>
Dodhe bel		Sal	<i>Shorea robusta</i>
Doodhi bel		Sendur	<i>Mallotus philippensis</i>
	<i>Holarrhena</i>		
Dudhi	<i>antidysentrica</i>	Shatavar	<i>Asparagus racemosus</i>
Ghatia	<i>Zizyphus xylopyrus</i>	Tendu	<i>Diospyros melanoxylon</i>
Girchi	<i>Casearia graveolens</i>	Tinsa	<i>Desmodium oojeinense</i>
Gohlar		Urena lobata	<i>Urena lobata</i>
Harra	<i>Terminalia chebula</i>	Van chana	<i>Flemingia semialata</i>

Response to comments for M.Sc. dissertation titled
**‘Assessing the synergistic effect of two invasive plants on
native plant communities in Kanha National Park, Central
India’.**

I thank the examiners for critical evaluation of my dissertation study and the comments posed. Thank you for acknowledging the research work as an important advance in the field of invasion ecology. Comments have been responded in a point wise manner and attached overleaf.

Rajat Rastogi
XV M.Sc. Wildlife Science
Wildlife Institute of India.

Forwarded by:

Prof Qamar Qureshi
Scientist-G
Co-supervisor

Date: 7 July 2017

Place: Dehradun

1. Good work!

Thank you! 😊

2. Without an experimental design, how do you know which direction the causality lies? I.e. are invasive species able to colonize the less fertile areas rather than cause the decline in fertility and associated diversity?

The ecological relationship between invasive plants and soil nutrients has been a topic of major concern, lately. Recent studies have showed that with increase in Lantana soil carbon and soil nitrogen has increased (Osunkoya & Perrett 2010). The present case study was an observational experiment and not a manipulative one, designed to compare the diversity parameters and edaphic factors in thirteen classes of Invasion given in table 1. To achieve this, the forest type was selected to be Sal (*Shorea robusta*) and extrinsic effects from canopy opening and different habitat type were controlled. In this way, any change in diversity and edaphic factors was considered to be an effect of invasive species only. However, I also agree that the relationship thus found is correlative and needs manipulative experimentation, which was beyond the scope of current study.

3. Discuss the limitations of intermediate disturbance hypothesis wrt operational definition in discussion section

The suggestion is accepted and I have incorporated critiques of IDH in the discussion (Page 39 and 40).

4. Replace all we with I, this is your thesis, you can put we in your research paper.

The suggestion has been incorporated in the revised thesis.

5. How did you select them? Describe in methods section.

Selection of these 120 study plots was done after surveying 56km² of Sal forest area. It was based upon the percent cover of invasive species, Flat terrain, similar canopy cover, distance from canopy openings, different forest types and water bodies. The selection criterion was mentioned in the method section, in the draft sent to the examiner.

6. Map with overlaid grids and selected grids would help in judging whether sampling was biased in any way

Map has been added as a part of appendix S3

7. *Location of transects and sampled grids are not visible in figure 3*

Map has been added as a part of appendix S3

8. *So you did 5613x3= 16800 plots in 5 months??*

Yes. For the first objective where various species distribution models are being tested, I along with my team covered 56 km² area and laid 15m radius plots for cover of invasive species, canopy cover and native trees specifically.

9. *Cite in correct format*

The comment has been addressed in the revised thesis. Please refer to page 9.

10. *Replace all 'we' by 'I', since this is an individual thesis, not the paper.*

The comment has been addressed in the revised thesis.

11. *Please defend this statement in the discussion, why should weed abundance not be the response variable?*

Decline in species diversity and richness due to invasive species has been recorded in many ecosystems. Similarly, with the current study design (as mentioned in the response to comment 2), I wanted to test the effect of these two weeds (*Lantana camara* and *Pogostemon benghalensis*) on native plant diversity and edaphic factors like Soil organic carbon, potassium, etc., and I assessed their effect on native species diversity by comparing 12 classes of single and multiple invasions with native class (uninvaded). I assume that the uninvaded plots provide a proper representation of diversity in Sal forest type for Kanha NP. Thus, weed abundance (lantana and pogostemon) is being used as the explanatory variables and not the response variable.

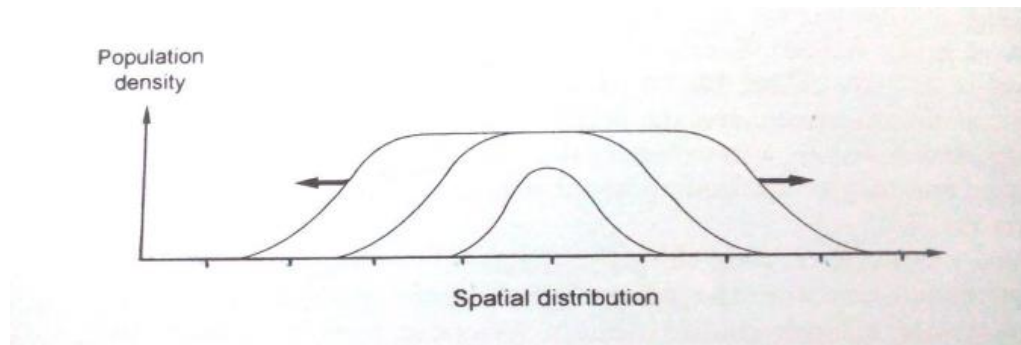
12. *About 70% of the sampled area*

The suggestion has been incorporated and I mentioned the percent occupancy for both the species in the revised thesis.

13. *If presence of lantana is best explained by presence of lantana in adjacent plot, does it mean that the 1 ha scale of sampling is not appropriate? Alternatively should you be correcting for autocorrelation?*

Presence of Lantana in sampling plot is best explained by presence of Lantana in the adjacent plot. This can be because of the reason that Lantana grows as a thicket. Density of one plant increases in an area and once the highest density is reached the plant spreads transversely as shown in the picture below (Williamson 1993). I assume that this thicket functions as the centre of spread from where the plant either spreads or is dispersed by various means (birds, mammals, insects, etc.). The scale of 1 hectare is put so as to ensure the availability of that spatial cell for sampling the biological aspect of that area (Vegetation sampling) and I feel that this scale is appropriate to study

distribution of invasive plants. Since percent cover of invasive species in the adjacent cells is taken into consideration, I corrected for autocorrelation.



14. If this is compared to the naïve estimate of 70% area, esp the BDM model, how do you explain the small area (approx. 25%) predicted?

The total study area is 231km², out of which 56km² (24%) area was sampled for cover of invasive plants. The estimate of 71% of area being invaded by lantana and 66% by pogostemon is based on the surveyed area of 56 km², whereas, the modelled distribution is for complete study area.

In the Biophysical density model (BDM), we used the physiological thresholds from the Biophysical threshold model (BTM) and incorporated densities of both invasive plants by using Bayesian density kriging. Each Species distribution models being used were further validated using 25% of the known data cells and checked for sensitivity and specificity indices. Taking $p < 0.05$ as the validation criterion, If the predicted and known presences showed an overlap or a difference, they were considered as presence or absence respectively.

15. Birds are not in the objective

The word 'Bird' has been removed from the revised thesis. Please refer to page number 25.

16. Use full variable names, and cut down on decimal places

Suggestion has been incorporated in the revised thesis. Please refer to page 30.

17. Can the difference be tested for significance?

I did not test the differences for significance but the means of response variables (diversity indices and edaphic factors) with standard errors. Also, the comparison for all the response variables was made between the uninvaded class and twelve classes of invasion (Table 1). The estimates of their errors is provided in the appendix S7

18. Are these the results of t-tests? Are the samples independent? Anything will be significant with a sample size of 5600 or 18000.

No, the results are of linear modelling in an ANOVA framework. The detailed table is given in appendix S7. The samples were independent in an spatial and design context.

For the second objective the sample size was 120 sampling plots. The sampling was considered to be completed when for all the vegetation taxa, species asymptotes were acquired.

19. Do you have estimates of error on the indices?

Yes, the error estimates are given in the appendix S7 with individual tables. For the ease in reading and understanding, I tried to make these tables coloured, where green colour signifies highest value decreasing to the colour red. And values which either decrease or increase significantly ($p < 0.05$) w.r.t. NPNL (uninvaded plots) are **BOLD**

20. Can you call 50% less? If there is correlation only after 50% what is the effect size?

I have corrected my statement here and less is replaced by 'lesser'. It is a relative connotation to the magnitude of invasion. Also, there have been studies mentioning about the threshold after which the dignificant effects of invasive species are found (75% in case of lantana).

21. Please rewrite this paragraph, it is not clear what you are trying to say.

The suggestion has been incorporated in the discussion section (Page 39 and 40).

22. In the light of the fact that this is an observational study, how do you account for the mechanism of these processes? How do the weeds do this?

I tried to make a theoretical context of the prospective mechanisms which might be underlying with biological invasions. I observed the increased abundance of nitrogen and calcium fixing plants when lantana was present in higher abundance. Which, I feel can be an indication towards the patterns of altered nutrient dynamics, where, N-C ratios in soil changes leading towards a homogenized community dominated by few common species. This can be attributed to the theoretical explanation that invasive plants take in resources from soil and alter with the nutrient cycling, they are also found to have deleterious impacts on native biodiversity (as mentioned in the previous answers). These theoretical phenomena have been tested and affirmed by various studies (Ehrenfield 2001, Ehrenfield 2003).
