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Predicting the distribution and abundance of invasive plant species in a sub-tropical woodland-grassland ecosystem in northeastern India

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Abstract Invasive plant species have become increasingly problematic in tropical and sub-tropical ecosystems, with the potential to decrease native plant diversity, increase fire occurrence, and cause ecosystem degradation. Numerous factors including disturbance due to fire, grazing, roads, human activities, reduction of native diversity, and soil fertility are known to influence invasibility of a habitat and/or promote the spread of invasive species. We studied invasive species distribution and abundance in a 519 km^2 wildlife reserve that has sub-tropical woodland and grasslands. We sampled 134 plots of size 30 × 30 m^2 and found that *Mikania micrantha* (a climber) and *Chromolaena odorata* (a shrub) were the most prominent invasive plants. We then tested the influence of eleven environmental variables that are either direct measures or proxies of resource availability, vegetation density, disturbance, and moisture stress. Using these predictors, we performed a decision-tree-based regression and prediction to test the influence of these variables on invasive species abundance and to generate distribution maps. The model had significant predictive power in the case of *Mikania* (R^2 = 0.469) but was poor for *Chromolaena* (R^2 = 0.056). Annual precipitation, soil phosphorus, and vegetation attributes had a significant influence in *Mikania*, and fire frequency had the strongest influence on *Chromolaena*. We could not quantify direct disturbance such as cattle grazing and resource extraction, which could add to the predictive power for these species. Given that invasive species continue to expand in range and abundance, more directed ecological monitoring and analyses are needed to manage ecosystems under the threat of invasions.

Keywords Invasive species · Woodland–grassland · *Mikania micrantha* · *Chromolaena odorata* · Manas National Park

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Introduction

The rapid spread of invasive alien plant species (hereafter invasive species) in recent decades has become a major concern in many sub-tropical and tropical ecosystems (Foxcroft et al. 2010; Vilà et al. 2011; Foxcroft et al. 2017). Invasive species have the potential to disrupt native plant community structure, decrease forage availability for herbivores, reduce species diversity, and degrade ecosystem function (Mack et al. 2000; Hejda et al. 2009; Powell et al. 2011; Sankaran et al. 2014; Joshi et al. 2015; Thapa et al. 2016; Schirmel et al. 2016; Early et al. 2016; Bellard et al. 2016). Although there were reports that rates of new introductions of alien species may have peaked decades ago (Tye 2001), recent analyses show no evidence for saturation in the accumulation of invasive species worldwide (van Kleunen et al. 2015; Seebens et al. 2017). Dramatic increases in range and abundance of invasive species were reported long ago (Everett 2000; Mack and Lonsdale 2001), leading to extensive worldwide research on the factors that facilitate expansions of invasive species (Stohlgren et al. 1998; Fridley et al. 2007; Barbosa et al. 2010; Spear et al. 2013; te Beest et al. 2015b; Diekmann et al. 2016; Seebens et al. 2018), and also in predicting their future distributions (Gallien et al. 2010; Adhikari et al. 2015; Mainali et al. 2015).

Although humans have been largely responsible for introductions of non-native species in different parts of the world (Cassey et al. 2005; van Kleunen et al. 2015), the invasibility of different types of ecosystems to invasive species is less certain. Theoretical studies on invasibility have examined a wide range of processes from fluctuating resources, tolerance- and suppression-based competition, and the availability invading propagules or propagule pressure (Davis et al. 2000; MacDougall and Turkington 2005). Empirical studies on invasibility of different ecosystems have implicated riparian habitats as havens or corridors of exotic invasions (Stohlgren et al. 1998; Truscott et al. 2007), but other research has shown that quantifying propagule pressure is critical for assessing the role of habitat (Eschtruth and Battles 2011). Whether native species diversity itself influences invasibility has long been debated, and although it is appealing to think that high native species diversity confers resistance to invasion, the relationships between native species numbers and the number of species or relative success of exotics appears to vary with scale. The observed negative relationships at fine scale and positive relationship at large/regional scales (Kennedy et al. 2002) have been termed the 'invasion paradox' (Fridley et al. 2007). On one hand, the factors that favour plant growth at large scales in species-rich regions may help both native and exotic species alike, with the added risk that any reduction in native species richness may benefit invading species. At small scales, however, local species richness appears to restrict both the numbers of invasive species and their proportions in the community (Kennedy et al. 2002).

There is more compelling evidence for the role of disturbance, and observations show that open and disturbed forests are more susceptible to invasion, particularly with the altered vegetation and microhabitat characteristics that accompany forest degradation (Cadenasso and Pickett 2001; Pyšek et al. 2002; te Beest et al. 2015b). However disturbance typically also affects diversity, so the relationships between invasibility on one hand and disturbance and diversity on the other need to be carefully examined (Clark and Johnston 2011). Established native plants may provide invasion resistance even under disturbance and high propagule pressure (McGlone et al. 2011), but such a relationship may vary temporally with disturbance (Clark and Johnston 2011). Nevertheless, the decline in tree density by fire and clearing of vegetation leads to the opening of habitats and facilitates invasions (te Beest et al. 2012). Such changes in vegetation structure may also lead to the increased availability of light and soil resources, which invasive species may exploit with greater abilities for light capture (te Beest et al. 2015a) or nutrient acquisition (Sardans et al. 2017). Persistent disturbance to natural ecosystems is usually associated with increased human activities and appears to have a strong influence on both plant and animal invasions (Spear et al. 2013).

In addition to habitat factors, the specific life historical attributes that may give invasive species a competitive edge and determine their success have also been widely investigated. Photosynthetic rate, water- and nutrient-use efficiency, resistance or tolerance to herbivory, disease, and fire are physiological attributes where non-native species may score over resident species (van Kleunen et al. 2010). Studies, however, do not provide unequivocal support for superior life history strategies of invading species but point to how these species exploit changed conditions. For example, in *Chromolaena odorata* (L.) R. M. King and H. Robinson (Asteraceae), a noxious non-woody sub-shrub widely prevalent in the tropical and subtropical ecosystems, photosynthetic traits indicate moderate shade-tolerance and ability to grow in moderate shade, but its expansion is only rapid in open and disturbed habitats (Quan et al. 2015), with modified resource allocation under disturbance (te Beest et al. 2015b). Therefore, ecosystems that are heavily impacted by disturbance tend to be affected in numerous ways, and invading species may simply exploit the changed conditions that may be more limiting to native flora (Didham et al. 2005; MacDougall and Turkington 2005). In the short term, the release of nutrients and space due to disturbance may facilitate invasion under high propagule pressure (Catford et al. 2011) by providing a 'niche opportunity' to invasive species (Shea and Chesson 2002).

Here we study invasive plant species, in Manas National Park, a protected wildlife reserve located in the Himalayan foothills in northeastern India. This is an important wildlife habitat, and the high diversity of mammal and bird species that occur here may in part be due to the heterogeneous vegetation mosaic of subtropical forest, grasslands, and woodland–grasslands composed of different species (Sarma et al. 2008). Field observations by forest managers and researchers indicate that invasive species may be increasing in range and abundance, but there are only a few reports (Lahkar et al. 2011) (Choudhury et al. 2016) (Adhikari et al. 2015). Although particular invasive plant species distributions may span regional and sub-continental scales (Barik and Adhikari 2012), the clue to understanding their expansions in range and abundance may lie at smaller (landscape) scales, where alterations in vegetation and land-use may have rendered ecosystems more prone to invasion. Thus, it remains unclear why invasive plants have spread rapidly in Manas National Park, as recent observations indicate (Lahkar et al. 2011).

We conducted field measurements of invasive species abundance in sample plots located across Manas National Park and used these data in a statistical model to test the importance of climatic, soils, vegetation, and disturbance from fires, roads, and edge effects, as determinants of invasive species abundance. Using this model in combination with raster maps of climatic variables, vegetation, and soil nutrient levels for the entire park, we also predicted invasive species abundance for the entire landscape.

Materials and methods

Study area

Manas National Park (MNP) is a 519 km^2 protected area located at the foothills of the Bhutan Himalayas (26°35′–26°50′N, 90°45′–91°15′E) under Bodoland Territorial Council of Assam, India (Fig. 1). It is bounded to the north by dense sub-tropical forest in the contiguous Royal Manas National Park in Bhutan. To the south of MNP are thickly populated villages and agricultural land, while the eastern and western boundaries are contiguous with reserve forests that are largely fragmented and subject to different levels of human use. MNP is a protected area, a UNESCO World Heritage site, and part of a designated Tiger and Elephant Reserve. Despite this protection, local communities extract forest resources including grasses and reeds and graze their livestock in some parts adjacent the southern boundary. Forest managers continue to use grass fires during the dry winter months to prevent woodland invasion of grassland sites, but this is not done systematically. Cattle grazers may also set fire to promote fresh growth of grass and rid the ground of dry unpalatable biomass. The climatic conditions prevalent in the region are characterized by the Indian monsoon (Takahata et al. 2010), which brings extremely heavy rainfall (up to 3300 mm per year), most of which occurs during June to October. The temperature varies between a mean maximum of 37 °C in summer, and while minimum temperatures of 5 °C have been recorded in the winter, the values are typically higher. The winter dry season starts in November and lasts until the occurrence of the pre-monsoon showers in March or April.

Field methods

We installed a total of 134, 30 m × 30 m plots located across the 519 km^2 area of MNP. Although plot locations were chosen randomly, some locations had to be altered slightly because of difficulty in access caused by dense undergrowth, swampy conditions, and international border regulations at the northern boundary. Furthermore, Manas River flows in a north–

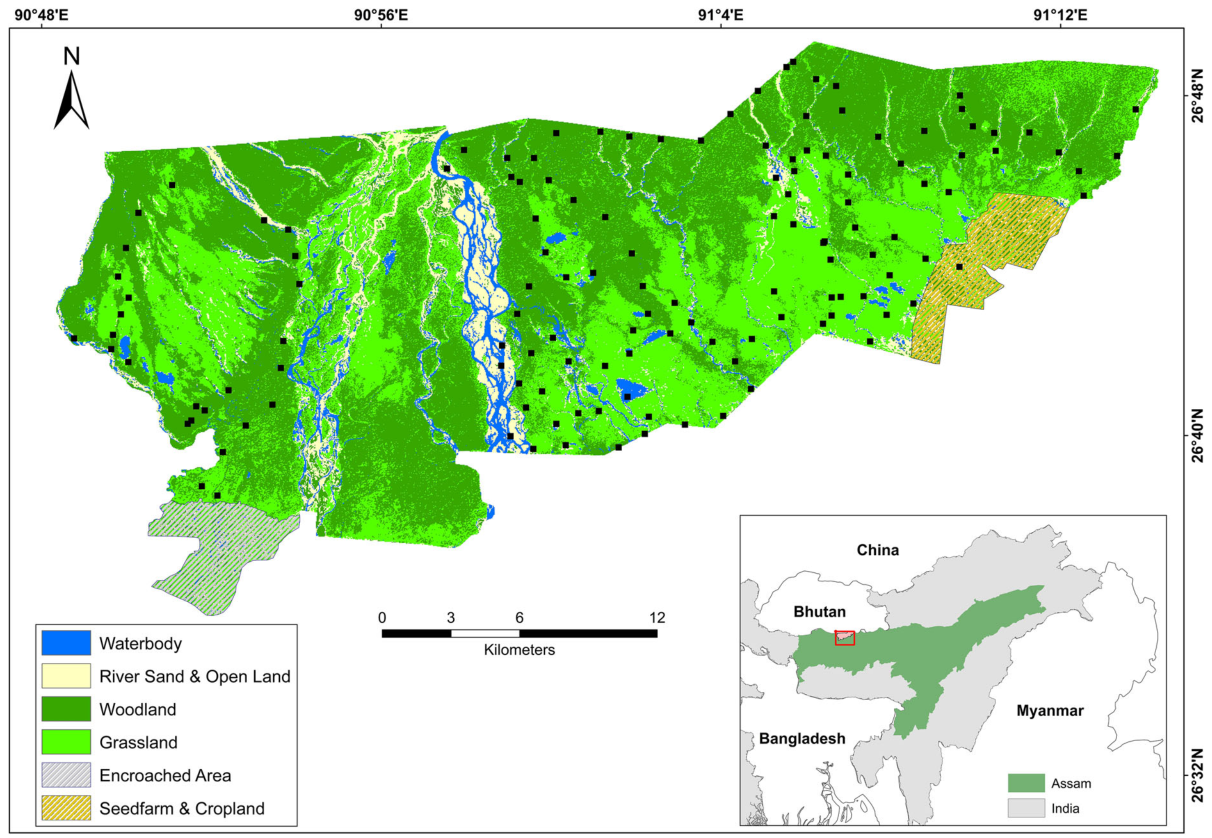

Fig. 1 Location map of Manas National Park, in Assam, northeastern India

south direction in the west of the centre of the park and has changed course several times in recent decades leaving large areas as sand banks with sparse or no vegetation.

In each 30 m × 30 m sampling plot, we identified and counted all woody plants of size ≥ 1 cm diameter at breast height (DBH), with the exact DBH measured for each individual. However, plots in grasslands often had no woody plants of size ≥ 1 cm DBH were present. Here the major component was typically the grasses, and grasses were sparsely present in plots dominated by trees. To sample grasses, we distinguished between tall grass species (> 1.3 m height at maturity) and shorter grass species (< 1.3 m height) and used different sampling designs for each. For tall grass species, we counted the number of identifiable clumps of each species. For shorter grasses, herbaceous species of angiosperms, and ferns, we installed two sub-quadrats of size 10 m × 10 m inside each 30 m × 30 m plot and identified and counted all individuals of the herbs, and the number of clumps for the grasses.

In each vegetation plot, we also estimated the abundance of invasive plant species. Although several invasive species are known to occur in and around the MNP region, only two species—*Chromolaena odorata* (L.) King & H.E. Robinson and *Mikania micrantha* Kunth—were noticeably abundant, so we restricted our study to the two species. These species have also been recognized as invasive species that pose a serious threat to natural vegetation in several parts of India, ranging from hills to the plains (Sankaran et al. 2014). *Chromolaena odorata* (hereafter *Chromolaena*) is a perennial shrub species in the Asteraceae that is native to the neotropics, with its range stretching from southern Florida to the upper drainage basin of the Amazon in southern Bolivia. It has spread rapidly after being introduced into India during the second half of the last century (Gautier 1992). IUCN's Invasive Species Specialist Group has identified *Chromolaena* as one of the hundred worst invaders. A survey of the density of invasive species in MNP found that the density of *C. odorata* was highest among invasive species in the park's central grasslands—ranging from 9.4 to 15.1 plants per m^2 (Lahkar et al. 2011). *Mikania micrantha* (hereafter *Mikania*) is a perennial creeping climber known for its vigorous and rampant growth, high reproductive rate (sexual and asexual), and appears to grow best where fertility, organic matter, soil moisture, and humidity are high. It is native to tropical and sub-tropical Central and South America and was introduced in India after World War II, and has colonized regions where successional forests are common (Swamy and Ramakrishnan 1988).

To estimate invasive species abundance in each of the 134 sampling plots, we randomly chose three 5 m × 5 m sub-quadrats within each plot. Within each sub-quadrat, we enumerated the two invasive species as the number of clumps. In both species, individuals cannot be unambiguously identified, so we could only count the numbers of clumps. Clump sizes varied only slightly, so we were able to count the numbers of clumps reliably in different quadrats. Using these average density data for the three sub-quadrats, we expressed the average density for each species in each 30 m × 30 m plot.

Environmental predictors of invasive species distributions and abundance

We tested several environmental variables as predictors of invasive species distributions and abundance in MNP. To test soil fertility, we measured three soils nutrient variables (Nitrogen, Phosphorus, and Potassium) using topsoil samples obtained from the vegetation plots. We obtained mean annual precipitation data from a global dataset (Hijmans et al. 2005), and we derived three variables from remotely sensed data. These include fire frequency to characterize recent fire history, Normalized Difference Vegetation Index (NDVI) to represent vegetation, and Normalized Multi-band Drought Index (NMDI) to capture dry-season moisture stress. Each of these variables was derived for the entire MNP landscape of 519 km^2 as raster images at 30-m resolution.

For the three soil variables, we collected and analysed topsoil samples from 117 of the 134 plots during December 2013. We could not collect soils from the other plots due to difficulties in access during soil sampling. We collected about 200 g of topsoil (top 20 cm) away from tree stems roughly in the middle of each plot. Total soil nitrogen was estimated using the oxidative release of N by alkaline potassium permanganate (Sahrawat 1982). For soil phosphorous concentration, the colourimetric method (Bray and Kurtz 1945) was used, and for potassium concentration flame photometric analysis was carried out (Isaac and Kerber 1971).

We obtained NDVI at ~ 30-m resolution using Landsat TM/ETM + data from the year 2012. NDVI is widely used to quantify vegetation cover using remote sensing (Pettorelli et al. 2005). Vegetation absorbs red light and reflects back in the near-infrared, and this extent of scattering is dependent on vegetation conditions (e.g., leaf area index). The differential reflectance of near-infrared and red band emission is measured by the optical sensor of the satellite and used to determine NDVI. It ranges from − 1 to + 1; a large negative value represents the lack of vegetation (e.g., water bodies), and values approaching + 1 indicate dense forest with high leaf area index. Since NDVI is associated with vegetation greenness, it changes with the season, typically peaking after the monsoon and being lowest towards the end of the dry season. We derived NDVI for pre-monsoon (January/February) and post-monsoon (November) dates and used both of these as predictors. NMDI is an indicator of the moisture content of soil and vegetation (Wang and Qu 2007). Increase in soil moisture content and leaf water content results in reduced reflectance of short-wave infrared (SWIR) radiation, which is used to compute the drought index. NMDI was similarly derived from Landsat TM/ETM + bands, for the month of February, which is the peak of the dry season. To obtain relatively unbiased estimates for NDVI and NMDI, we derived these variables for three years (2011–2013), and used the median value of the three years for each pixel to derive a pre-monsoon NDVI map, a post-monsoon NDVI map, and a peak dry-season NMDI map (See Supplementary Material for further details on the satellite data and the maps for these predictors).

Fire frequency data were obtained from MODIS fire products that are available from the MODIS repository (Justice et al. 2002). The MODIS satellite sensor obtains information on the occurrence of fire at a spatial resolution of 500 m once every 15 days, and this time series is available starting year 2000. We obtained such fortnightly records of the presence of fire for the period 2000–2012 for MNP and computed the frequency of fire for each 500 m pixel for this time interval. This is a measure of the burden of fire during this period. Although forest managers have been using controlled dry-season ground fires for decades, they do not maintain systematic records of burning. It was therefore impossible to obtain direct estimates of fire frequency from forest department records. We, therefore, used MODIS fire frequency for each 500 m pixel and generated a raster of fire frequencies for the entire park (see Supplementary Material). A similar approach has been used to derive fire frequencies for MNP for an earlier period (Takahata et al. 2010). Finally, we derived the elevation map and the elevation for each sampling site using the ASTER Digital Elevation Model (https://www.ersdac.or.jp/GDEM/E/3.html).

Roads and habitat edges can act as conduits for invasion, both by opening habitat and through increased human activity (Barbosa et al. 2010). We, therefore, digitized the road network and created raster maps (30-m resolution), where each pixel value was the distance to the nearest major road. We also created a similar raster as a function of distance to the southern park boundary (other boundaries are contiguous with forest and not human settlements). All told, we had 11 environmental predictors, and the rasters of these predictors are presented in Supplementary Material.

Using log-transformed values of invasive species abundance in 134 plots and the corresponding values of environmental/habitat predictors, we computed multiple regressions for both *Mikania* and *Chromolaena*. This was done to identify the nature and strength of the effects of these predictors on invasive species abundance.

Predicting invasive species distributions for the MNP landscape

We used a statistical model of invasive species abundance measured in 134 vegetation-sampling plots to predict invasive species distributions and abundance for the MNP landscape. We did this by using the Random Forest regression and prediction framework, an ensemble-based decision-tree algorithm for classification and regression (Cutler et al. 2007), available as a software package 'randomForest' (Liaw and Wiener 2002) in R Development Core Team (2011). To do this regression, we first randomly partitioned the dataset of 134 plots into a *training* dataset with 100 plots and a *testing* dataset with 34 plots. We then computed Random Forest regression for each invasive species with the training data set, using clump density (log-transformed values) of the species as the response variable, with the corresponding predictor values extracted from the 'stack' of raster files of the predictors. Since this is an ensemble-based decision-tree approach, we had to set the number of trees that would be computed. Typically, 500–1000 trees are computed, and we set the number of trees at 801, choosing an odd number so that ties could be settled without ambiguity. The 'randomForest' regression computation simultaneously involves the testing dataset (here 34 data points), and the mean squared error and R^2 in applying the fitted regression model on the test data are also obtained.

We computed the importance of each of the predictors towards the regression, using the *variable importance* function available in 'randomForest'. This works by dropping one variable at a time from the regression and computing the percentage increase in mean squared error (MSE) of the regression. Finally, we used the regression model to predict invasive species abundance and distributions for the entire MNP landscape at 30-m resolution. The 'predict' function in 'randomForest' uses the computed regression and the raster maps of the environmental variables to predict invasive species abundances for the entire landscape.

Results

We recorded 35 tree species and 80 non-tree plant species (woody shrubs and herbaceous plants, including three species of ferns) in the entire dataset of 134 plots. Diversity at the family level was high, with 20 families among tree species and 41 families among non-tree plants, accounting for a total of 51 families in all. Fabaceae was the most diverse family among trees with five species, while Poaceae with 19 species was the most diverse family among non-tree plant species. Tree density was generally low and had a skewed distribution among plots. In all, 118 plots had at least one individual tree $\geq$ 1 cm DBH, with a median density of just 12 trees in a 30 m × 30 m plot. *Lagerstroemia parviflora* was the most abundant tree species and was also the most frequent, followed by

Dillenia pentagyna, *Bombax ceiba*, *Trewia nudiflora*, and *Terminalia bellirica*, in decreasing order of abundance.

Among non-tree plant species that included mainly grasses and shrubs, and the two focal invasive species *Mikania* and *Chromolaena* were present in 108 and 93 plots, respectively. Among grasses, *Saccharum narenga* was the most widespread, occurring in 86 plots, followed by *Ophiuros megaphyllus*, *Bambusa arundinacea*, *Phragmites karka*, and *Arundo donax* in decreasing order of abundance. Notably, species of *Saccharum* like *S. spontaneum* and *S. ravennae* were rare in our plots. Overall plant species richness within plots was approximately normally distributed among plots, with a range of 3–27 species (excluding the invasive species) and median species richness of 16.

Multiple regressions of invasive species density with 11 environmental/habitat predictors were statistically significant for both *Mikania* (Adj. $R^2 = 0.511$, $p < 0.001$) and *Chromolaena* (Adj. $R^2 = 0.124$) (Tables 1, 2). Four variables (mean annual precipitation, DistBound, fire frequency, NDVI post-monsoon, soil phosphorus) showed significant predictive power for *Mikania* ($p < 0.05$ for all), and only two variables (fire frequency, elevation) were significant for *Chromolaena* ($p < 0.05$ for all), and NDVI pre-monsoon had a p value of 0.051 (Tables 1, 2).

The Random Forest regression with *Mikania* density as the response variable and 11 environmental or habitat variables as predictors (see Supplementary Figs. S1 through S11) resulted in an R^2 value of 46.93%, expressed as the percentage of variance explained. The percentage of the variance explained for the smaller testing dataset was lower at 34.57. The variable importance analysis shows that annual precipitation was the most important predictor, with over 30% increase in MSE of the regression when it was dropped from the list of predictors. The variable importance plot (Fig. 2) depicts the predictive power of all 11 variables, and three other variables, soil phosphorus (15%), elevation (14%), and post-monsoon NDVI (10%) led to greater than 10% loss of accuracy when excluded. Notably, excluding fire frequency had little effect (1.4% reduction in MSE)) when excluded from the regression.

The Random Forest regression for *Chromolaena* density as a function of the nine environmental or habitat predictors yielded an R^2 value of 5.66, expressed as the percentage of variance explained. This value for the testing dataset was 7.95%. These two numbers are low, and the variable importance plot (Fig. 3) shows that none of the variables had a strong influence on *Chromolaena* density. Fire frequency had the maximal influence, with about 12% loss of accuracy upon excluding this variable, but since the

Table 1 Multiple regression of log-transformed values of *Mikania micrantha* abundance per 30 × 30 m^2 quadrat for 134 quadrats

Coefficients	Estimate	SE	t value	Pr(> |t|	Sig
(Intercept)	2.829	0.295	9.577	< 2e−16	***
Annual precipitation	– 4.207	0.732	– 5.750	0.000	***
Distance to boundary	1.032	0.440	2.346	0.021	*
Elevation	0.634	0.752	0.843	0.401	
Fire frequency	– 1.509	0.422	– 3.573	0.001	***
NDVI post-monsoon	1.270	0.495	2.565	0.012	*
NDVI pre-monsoon	– 0.893	0.651	– 1.371	0.173	
NMDI	0.429	0.420	1.021	0.309	
Distance to roads	– 0.131	0.318	– 0.411	0.682	
Soil nitrogen	– 0.129	0.385	– 0.335	0.738	
Soil phosphorus	– 0.782	0.338	– 2.314	0.022	*
Soil potassium	0.560	0.381	1.471	0.438	

Eight environmental/habitat predictors of invasive species abundance were used. Residual standard error: 3.42 on 122 degrees of freedom Multiple R-squared: 0.5516, adjusted R-squared: 0.5112

F-statistic: 13.64 on 11 and 122 DF, p value: < 2.2e-16. Significance levels are 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 2 Multiple regression of log-transformed values of *Chromolaena odorata* abundance per 30 × 30 m^2 quadrat for 134 quadrats

Coefficients	Estimate	SE	*t* value	Pr(> |t|	Sig
(Intercept)	1.065	0.437	2.439	0.016	*
Annual precipitation	− 1.927	1.082	− 1.781	0.077	
Distance to boundary	− 0.440	0.650	− 0.676	0.500	
Elevation	2.446	1.112	2.199	0.030	*
Fire frequency	− 2.237	0.624	− 3.582	0.000	***
NDVI post-monsoon	0.576	0.732	0.787	0.433	
NDVI pre-monsoon	− 1.895	0.962	− 1.968	0.051	
NMDI	− 0.786	0.622	− 1.264	0.209	
Distance to roads	− 0.054	0.470	− 0.116	0.908	
Soil nitrogen	− 0.028	0.569	− 0.049	0.961	
Soil phosphorus	− 0.593	0.500	− 1.187	0.238	
Soil potassium	0.714	0.563	1.268	0.207	

Eight environmental/habitat predictors of invasive species abundance were used. Residual standard error: 5.057 on 122 degrees of freedom. Multiple *R*-squared: 0.1969, Adjusted *R*-squared: 0.1244, *F*-statistic: 2.718 on 11 and 122 DF, *p* value: 0.0036. Significance levels are 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

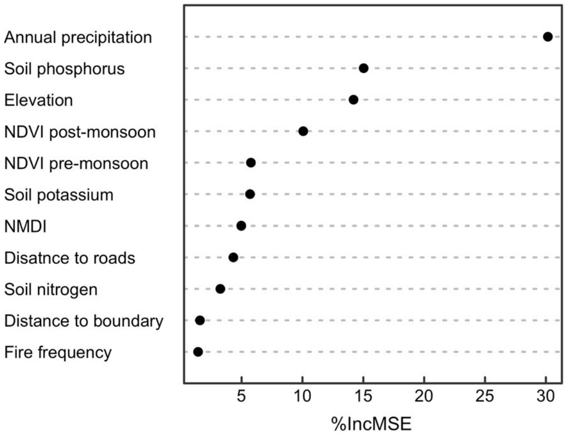

Fig. 2 The variable importance plot for *Mikania micrantha* obtained from Random Forest regression. The *x*-axis indicates the percentage increase in mean squared error on dropping the given variable from the regression

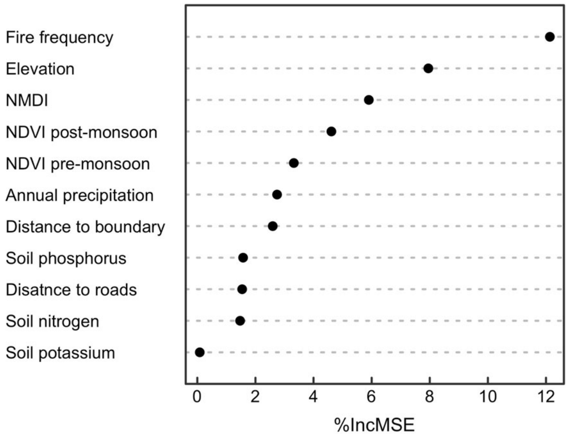

Fig. 3 The variable importance plot for *Chromolaena odorata* obtained from the Random Forest regression. The *x*-axis indicates the percentage increase in mean squared error on dropping the given variable from the regression

overall explanatory power was low, the importance of fire is insignificant. All other variables had lower than 10% influence on the regression.

We used the Random Forest regression for spatial prediction only for *Mikania*, as the regression had no significant predictive power for *Chromolaena*. The raster map at 30-m resolution for *Mikania* density across MNP shows widespread areas of relatively high densities in the eastern part of MNP covering almost two-thirds of the area, as well in the southwest of the park (Fig. 4). The northwestern corner shows a distinctly lower density than other parts. Other areas that show a low density of *Mikania* are encroached parts of the park that have little natural vegetation.

Since we could not derive a predictive model for *Chromolaena*, we just used the inverse distance-weighted interpolation to generate a density map for the MNP landscape (Fig. 5). This map shows that *Chromolaena* occurs at relatively low densities (compared to *Mikania*) across most parts of the park, with

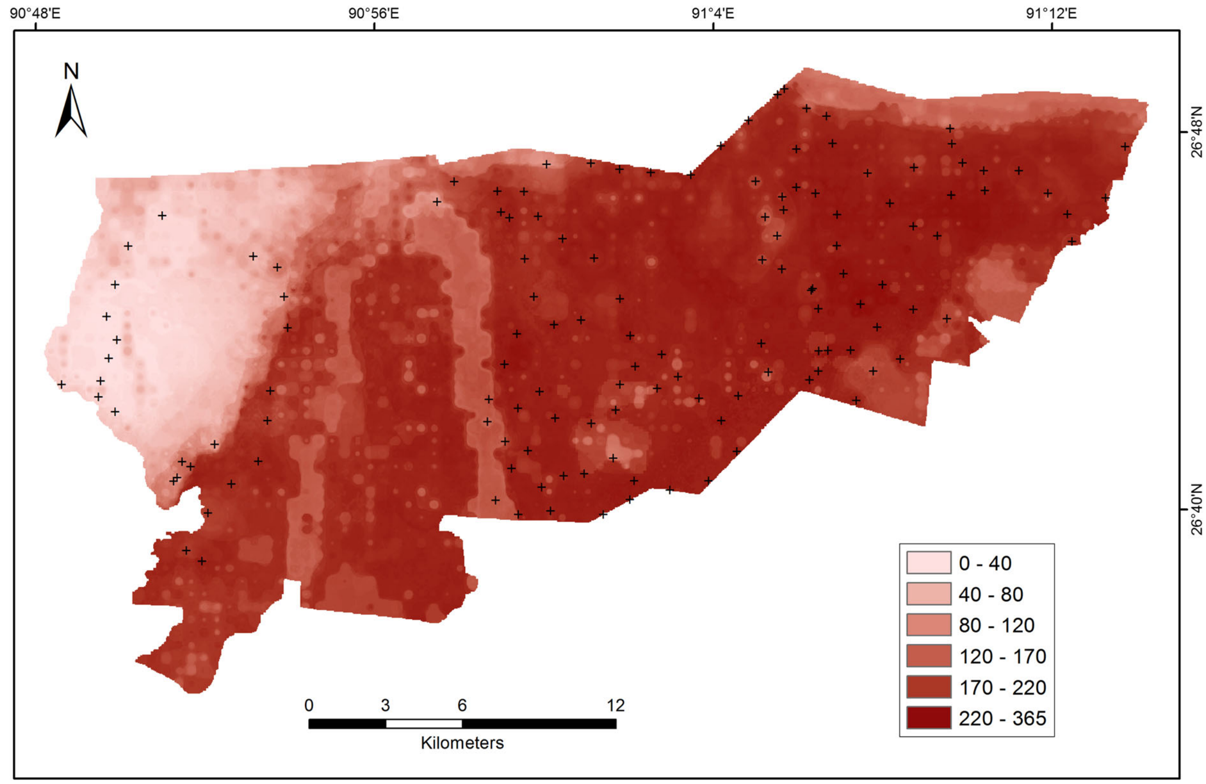

Fig. 4 The predicted density map of *Mikania micrantha* in Manas National Park obtained from Random Forest regression and prediction. The numbers indicate the number of clumps per 30×30 m^2 quadrat area. The points (" + ") indicate sample quadrat locations

some high-density patches near the south-central boundary and the northeastern boundaries. *Chromolaena* is generally widespread in the park, but our results show that it is present at rather uniform densities in most parts except near park boundaries in the south-central and northeastern parts of the park, where densities are clearly higher.

Discussion

We studied the influence of eleven environmental/habitat factors that potentially influence the abundance and distribution of two invasive plant species in a subtropical forest and woodland–grassland ecosystem and found that in only one species, *Mikania micrantha*, some of these factors were significant predictors of distributions and abundance. In the case of the other invasive species, *Chromolaena odorata*, none of the environmental/habitat factors explained abundance and distribution in the landscape to a significant extent. The results from Random Forest regression were only partially consistent with standard parametric multiple regression, but the overall statistical explanatory power levels were comparable. Our findings broadly mirror those of other more comprehensive studies predicting invasiveness, and the general conclusion is that "few or no factors allow consistent prediction of invasiveness" or of the distributions of adventive species (Thuiller et al. 2006). Although species distribution modelling for invasive species is particularly challenging (Václavík and Meentemeyer 2009), recent studies with large-scale data have shown high explanatory/predictive power of environmental variables (Shiferaw et al. 2019).

Studies on invasibility have focused as much on the life historical attributes of the species themselves (Quan et al. 2015; Canessa et al. 2018), as on the environmental factors that increase invasibility of habitats (Stohlgren et al. 1998; Sardans et al. 2017). We focused on environmental and habitat factors that

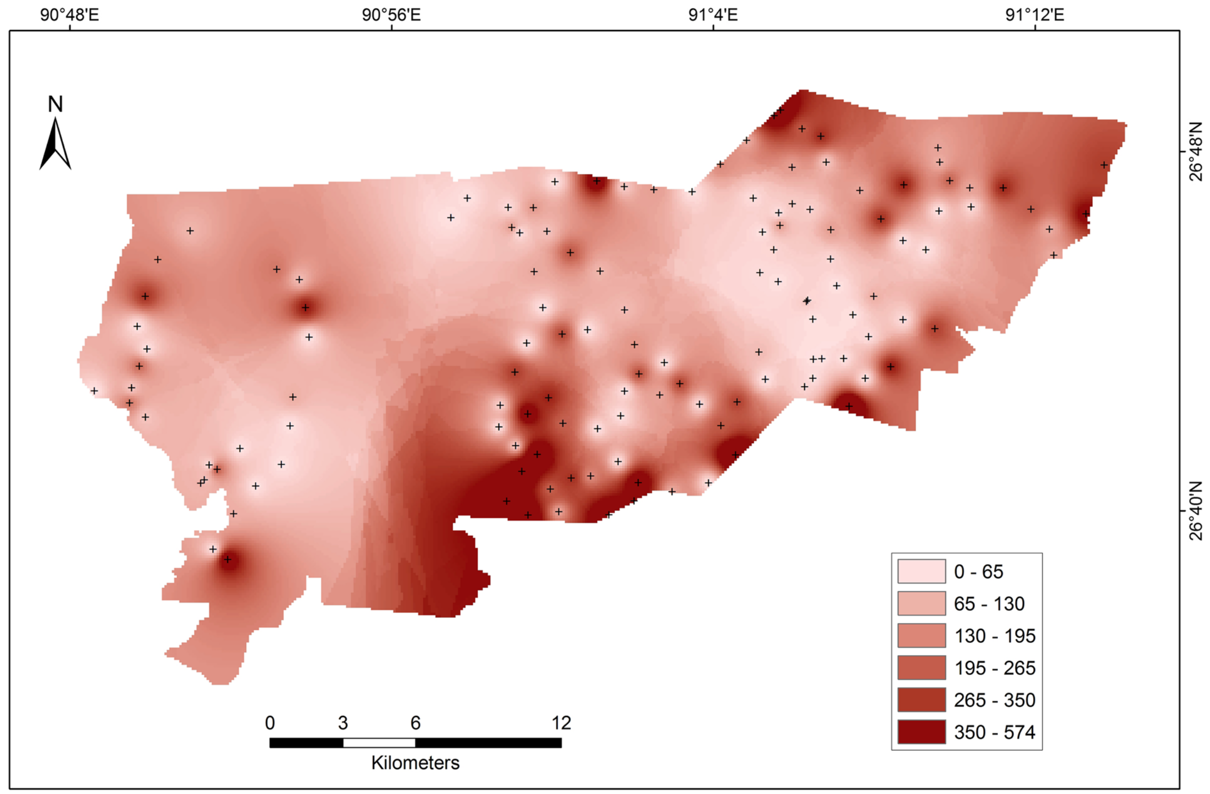

Fig. 5 The predicted density map of *Chromolaena* in Manas National Park obtained from inverse distance-weighted interpolation. Due to the poor fit, Random Forest based prediction was not done. The numbers indicate the number of clumps per 30 × 30 m^2 quadrat area. The points (" + ") indicate sample quadrat locations

are either direct measures or proxies of resource availability, vegetation density, disturbance, and moisture stress, variables that are known to influence invasibility of an ecosystem (Mack et al. 2000; Sankaran et al. 2014; Foxcroft et al. 2017). If these variables had a significant influence on the invasibility of an ecosystem, then the spatial distribution and variation in abundance of invasive plant species would be related to the spatial variation in these environmental and habitat factors. Our framework with explicit spatial data on invasive species abundance, spatial predictors, and a spatial regression framework had the statistical power to detect such a relationship between invasibility and environmental/habitat factors. Yet we found that our chosen environmental and habitat variables had only moderate power to explain the distribution of *Mikania* and almost no power at all to explain the distribution of *Chromolaena*.

Among climatic variables, we included only mean annual precipitation (Supplementary Fig. S1) in our study after examining several variables related to temperature and precipitation, because only annual precipitation varied substantially across the MNP landscape. Although the elevation range was small (20–290 m above mean sea level) (Supplementary Fig. S2), we believe this would determine the extent of the monsoonal floodplain and the level and duration of inundation. We also included another variable related to moisture availability or a drought index for the dry season, but this was a satellite-derived index (NMDI). We expect NMDI to capture some aspects of hydrology that total rainfall cannot capture because, despite the high rainfall, MNP has a strong dry season and complex hydrology because of streams and seasonal floods. We found that annual precipitation was a significant predictor of *Mikania* abundance, and the partial regression coefficient (Table 1) was strongly negative. Correspondingly, excluding annual precipitation from the list of predictors led to a substantial increase in the mean squared error of prediction for *Mikania*. High rainfall areas, therefore, had significantly lower densities of *Mikania* within this landscape. A significant influence of precipitation on *Mikania* has also been reported for another landscape in the region (Choudhury et al. 2016). For *Chromolaena*, however, annual precipitation was not a significant predictor, but even the overall statistical predictive power was low for this species. NMDI had negligible power to predict the abundance of both species, despite considerable variation in NMDI across MNP (Supplementary Fig. S9). *Mikania* generally grows on tree canopies but is rare in an intact tropical forest with low disturbance to the canopy. The negative correlation with annual precipitation may reflect variation in disturbance to forest canopies that tend to be more prevalent in drier sites. *Chromolaena* is a shrub and is known to expand rapidly in open habitat (Quan et al. 2015). At large scales, climatic factors are bound to play a dominant role for *Chromolaena* (Barik and Adhikari 2012), or for any other species, but predicting the spread and abundance of *Chromolaena* at landscape scales remains a challenge.

Although precipitation does vary across MNP (Supplementary Fig. S1), it is high enough in all parts of MNP to support tree-dominated vegetation. Instead what we find is a complex mosaic of pure grassland (of both alluvial tall grasslands and dry short grasses), woodland–grassland systems dominated by fast-growing early successional tree species, and even late successional tropical moist forest. Tree densities were low in woodland patches, while dense tropical moist forest was mostly present in small patches at the northern boundary, which is contiguous with protected forest in Bhutan's hills, where it is present as mid-elevation broadleaf forest (Champion and Seth 2005). Our sample plots did not capture the species richness of the older tropical moist forest, as they mostly occur across the border in Bhutan, but the background vegetation is a highly complex and heterogeneous mosaic against which the distributions of invasive species need to be understood.

At low elevations, factors including dry-season fires, grazing, hydrology, and historical land-use associated with human activities may all have been important in shaping the vegetation, as is known from grassland and woodland systems in general (Sankaran et al. 2004; Bond et al. 2005; Sankaran 2005; Sarma et al. 2008). Given the multitude of probable factors that influence vegetation structure in MNP, it is not surprising that annual rainfall and elevation (indirectly the floodplain) have only moderate predictive power in the case of *Mikania*, and almost none in the case of *Chromolaena*. However, we were surprised to see that NMDI had little influence on these invasive species. Although MNP receives high rainfall, it has a strong and intense dry season, and NMDI was meant to capture the influence of this dry-season moisture stress. Although NMDI does vary, it may be low everywhere and therefore have no differential impact across the landscape.

Second to annual precipitation, soil phosphorus (Supplementary Fig. S5) had the strongest influence on *Mikania* abundance, but almost none on *Chromolaena*. As the multiple regressions showed, Mikania infestation was greater when soil phosphorus was lower. Soil phosphorus is critical for lowland ecosystems (Condit et al. 2013), but we do not have data on phosphorus limitation on growth in MNP. Soil nutrients are known to influence invasibility (Sardans et al. 2017) but often it is disturbance or other factors and not resource competitive ability that determines the spread of invasive species (Seabloom et al. 2003). At MNP, it is likely that the relationship of *Mikania* with soil phosphorus arises through the significant influence of soil phosphorus (Supplementary Fig. S5) on tree diversity and abundance (manuscript in preparation). The importance of tree density on *Mikania* abundance is also evident in the significant positive influence of post-monsoon NDVI (Supplementary Fig. S6). NDVI typically correlates strongly with the density of vegetation, so we expected to find a stronger relationship between NDVI and *Mikania* density. Further analyses based on detailed vegetation characteristics such as tree diversity, biomass, and physiognomy may reveal the determinants of invasibility of this plant community to *Mikania*. In *Chromolaena*, the pre-monsoon NDVI was negatively related (Table 2) but marginally non-significant ($p = 0.051$), which is consistent with the preference of this species for open fire-prone habitat with generally low NDVI values in the dry season. At small scales, however, the distribution of *Chromolaena* appears difficult to predict using static environmental and habitat factors. Human activities may be critically important for this species, but our data suggest that fires had the greatest impact on *Chromolaena*.

There is no doubt that fire has been an ecological factor in the history of Manas ecosystems, but the exact nature and impact of fires are uncertain

(Takahata et al. 2010). Remotely sensed data such as MODIS are valuable over large scales, but they do not date back long enough, and also only record events from which the spatial extent and intensity of fires cannot be reliably mapped. In the absence of ground-based primary data on fire occurrence and extent, relationships with satellite-derived fire history cannot be derived. Since the fire incidence records for MNP are not available in sufficient detail for cross-validation, we could not generate validated a fire history. However, MODIS fire records have been widely used (Langner et al. 2007), so we chose to include this in our study, despite the lack of ground data (Supplementary Fig. S3). Our multiple regression results showed that fire frequency has a significant negative influence on both *Mikania*, and *Chromolaena* (Tables 1, 2) but Random Forest analyses showed that fire had a negligible influence on *Mikania* (Fig. 2) while it had maximum influence on *Chromolaena* (Fig. 3). These results from multiple regression and Random Forest appear difficult to reconcile, but both methods had little explanatory power on *Chromolaena* distributions. Fire generally promotes the spread of *Chromolaena* (Barik and Adhikari 2012; te Beest et al. 2015b), but we could not explain *Chromolaena* distribution in MNP using these variables. *Mikania*, being a climber, does not persist in completely herbaceous sites where fire is most common but is generally found in early successional or moderately dense woodland, where fires are infrequent. This could explain the negative relationship with fire we see for *Mikania* in multiple regression, but Random Forest results indicate that fire was not important (Fig. 2). Fire in moist habitats may act as a stress factor and promote invasive species (Alpert et al. 2000), and widespread distributions of invasive species may, in turn, modify the fire regime of an ecosystem (Brooks et al. 2004). Given the uncertainties in our reconstruction of fire history and the strong impact of the dry season, the impact of fire on invasive species in MNP may resemble patterns found in dry habitats.

Soil nitrogen and potassium had little or no influence on invasive species abundance for both *Mikania* and *Chromolaena*. The soils of MNP are relatively nutrient-rich, given that they receive alluvial nutrient deposits from annual monsoon floods. However, the soils tend to have higher clay content and may make soil nutrients less available for plant growth. The importance of nutrient limitation on plant growth has not been investigated for MNP, and a wider range of soil nutrients other than just N, P, and K needs to be measured and mapped at greater accuracy and resolution, to study how they influence vegetation and its susceptibility to plant invasions. We found that soil phosphorus was important for Mikania, and points to possible broader influence of soils, but our data are insufficient to investigate this in detail.

Linear disturbances like roads and edge effects at habitat boundaries are known to have significant affect invasibility of habitats by creating openings as well promoting human activities (Barbosa et al. 2010; Spear et al. 2013). However, we found no significant influence of distance to roads or distance to the park boundary where human interactions were maximal. The road network in MNP has been highly dynamic, with roads being cut and often overgrown due to disuse. Besides, there are numerous temporary trails and seasonal small streams that dissect the landscape, so evaluating the influence of these linear disturbances is difficult, as they are highly variable in time.

The difficulty of predicting invasive species distributions in MNP using simple environmental and habitat variables is worrisome. Although we considered several variables that are generally considered important, our predictive power was low, particularly for *Chromolaena*. It is possible that we failed to include some key variables, particularly those related to human activities, and the fine-scale influence of fire and soil moisture. Besides, *Chromolaena* may be very dynamic over time (Witkowski and Wilson 2001), so a single time-point density may be difficult to explain using static environmental or habitat data. So both environmental and habitat factors, as well as distributions and abundance of invasive species, may also vary considerably from time to time. These limitations may have played a part in influencing the relationships we detected with our data. Furthermore, all these environmental variables may be of little importance if the spread of invasive species is more intrinsically determined by the reproductive attributes that may promote asexual expansion or induce high propagule pressure that may further interact with habitat and demographic factors (Warren et al. 2012). The intrinsic attributes of *Chromolaena* are well known and appear to indicate its intrinsic life historical attributes that may be promoting this species.

Despite the expansion of both Mikania and Chromolaena in MNP, their impacts on native plant species are not known. Negative impacts have been recorded in similar ecosystems (Thapa et al. 2016) and may be occurring in MNP as well. As invasive species continue to spread, our ability to control them will depend on our understanding of what factors promote invasion. In particular, if forest management practices are interacting with emerging environmental changes in ways that we do anticipate or understand, our ability to manage natural habitat degradation may be limited. The opening of the vegetation by fires, livestock grazing, collection of forest produce, and other human activities are known to be responsible in a variety of ecosystems (Ramaswami and Sukumar 2011), but we could not estimate these effects in MNP. This is a difficult challenge because these factors tend to operate over long periods of time, and systematic monitoring has not been carried out in the past. This is a serious limitation for understanding current ecological problems in MNP. Given some level of human activities cannot be avoided or that some global changes are inevitable, systematic regulatory mechanisms coupled with long-term ecological monitoring need to be initiated urgently to understand and tackle the problem of invasive species in this ecologically valuable landscape.

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