Management of Biological Invasions (2018) Volume 9, Issue 3: 357–367
DOI: https://doi.org/10.3391/mbi.2018.9.3.17

Open Access

Research Article

Fire regulates the abundance of alien plant species around roads and settlements in the Serengeti National Park

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Received: 16 January 2018 / Accepted: 1 May 2018 / Published online: 18 June 2018

Handling editor: Anna Gazda

Abstract

A large portion of East African ecosystems are officially protected, yet increasing wildlife tourism and infrastructural development are exposing these areas to invasion by alien plant species. To date there has been little quantification of alien plant species in the Serengeti National Park, Tanzania. In this study, we aimed to: (1) establish a list of common alien plant species; (2) quantify the frequencies of alien species near roads and settlements (i.e. tourist lodges and a campsite), and (3) estimate the abundance (plant cover) of alien plant species in relation to source activities (i.e. gardening) and park management (i.e. fire). In total, we detected 15 alien plant species in our surveys with an 80% probability of encountering an alien species within the first 50 m from a road or settlement. Overall, we found no difference in the presence of alien species near roads or settlements, but did find a significant decline in species presence with distance from these sources. Cumulative fire frequency was the most important factor influencing the abundance of alien species with the highest alien plant cover in areas with infrequent or no fires over the last 13 years. There was no difference in alien plant cover in relation to other commonly cited source activities, which may be due to the stronger influence of fire. Although the abundance of the majority of alien plant species was negatively related to fire, some species, notably *Tagetes minuta,* had higher cover with more frequent fires. Our results contradict findings from other African savannahs that suggest fire promotes invasive species and this is likely due to the species-specific interactions with fire. In the Serengeti, fire will be difficult to use as a management tool due to variable species response. Thus, we highlight that other management approaches such as physical removal and biological control agents can be implemented; however future work with these techniques should also consider the interaction of alien plant species with fire.

Key words: East Africa, fire management, non-natives, protected areas, savannah, tourism

Introduction

Alien plant species in protected areas are a serious concern for biodiversity and conservation as well as human health and local economies around the world (Lowe et al. 2000; Brooks et al. 2004; Pyšek and Richardson 2010). This concern is particularly acute in East Africa where protected areas are not only globally significant centers of biodiversity but also important sources of revenue via wildlife tourism. However, while the importance of biodiversity for both wildlife and human livelihoods and wellbeing is widely recognized, the response to alien plant species in East African savannahs remains largely underdeveloped (Braun 1973). Against this background, this study provides primary data on the presence of alien species in a major protected area with an established wildlife tourism trade in East Africa, namely the Serengeti National Park, Tanzania, as well as the potential mechanisms that facilitate the entry and spread of alien species in protected areas. Such baseline data on first-sightings and location of alien species is important in order to respond to new and emerging alien plant species (Mehta et al. 2007) and helps identify high risk areas to target preventative measures (Byers et al. 2002; Bukombe et al. 2013).

Tourism is a well-known pathway facilitating the introduction of alien plant species into protected areas. The impact of tourism on the introduction of alien plant species is often indirect through supporting services, namely accommodation and roads. For example, in a recent study Witt et al. (2017) surveyed 24 lodges and camps and along roadsides in the Masai-Mara National Reserve, Kenya, and detected a total of 245 alien plant species. Settlements are often hotspots of alien plant species, particularly during the initial phase of construction when material is imported into protected areas. Reports from Ngorongoro Conservation Area, adjacent to the Serengeti National Park, showed that problematic alien plant species such as *Datura stramonium* and *Argemone mexicana* are regularly found at settlement construction sites (Foxcroft et al. 2006). Often deliberate introductions occur during landscaping and gardening around a settlement. Alien species are planted for ornamental and hedge purposes (Taylor et al. 2012), for shade and fences (Wakibara and Mnaya 2002), and/or to produce fibers for clothing and equipment (Whinam et al. 2005). Gardens and ornamental plantings can be hotspots of alien plant species with 212 out of the 245 alien species in the Masai-Mara National Reserve found around lodge and staff house gardens (Witt et al. 2017). Disposal of garden waste can provide further problems as alien species can often escape from designated dumpsites, as seen in Kruger National Park, South Africa (Foxcroft et al. 2008).

Besides settlements, infrastructure development contributes to the spread of alien plant species in protected areas. Roads are seen to enhance the tourist experience by providing greater connectivity between people and wildlife. Yet, development of infrastructure has been shown to increase the number of alien plant species in protected areas (Mazia et al. 2001; Pauchard et al. 2003; Pauchard and Alaback 2004). Regular disturbance from roads during construction and maintenance generates bare ground gaps within the native plant canopy enabling alien species to colonize and establish (Mazia et al. 2001; Pauchard et al. 2003; Pauchard and Alaback 2004). Identifying the pathways of alien plant species introductions associated with settlement and roads will therefore be important to target management of these source activities. This is particularly important in the Serengeti National Park as visitor numbers and associated demands on accommodation and road use in the Park are predicted to increase in coming decades (Eagles 2003; Lekan 2011).

Habitat management within African protected areas may further enhance the abundance or spread of alien plant species. One of the main habitat management strategies in African savannahs is human-induced fire, which is used to promote vegetation regrowth and reduce shrubification. Similar to settlements and roads, disturbance by fire can facilitate colonization and establishment of alien species that have a ruderal strategy. For example, high fire frequencies (i.e. short return intervals) have been shown to facilitate colonization and establishment of alien plant species, mainly ruderal forbs, in a Zimbabwean savannah (Masocha et al. 2011). However, settlements and roads typically have the highest diversity and abundance of alien plant species (Foxcroft et al. 2006; Witt et al. 2017), yet they are often protected from fires through the use of fire breaks, for example by reducing the fuel load by slashing vegetation to ground level (Trollope et al. 2005). Therefore, the overall relationship between fire management and alien plant species occurrence and establishment remains unclear. Additionally, once established, alien plant species can also alter the fire regime. It has been shown that alien grass species can increase the fuel load of the invaded community and thus increase the frequency and intensity of fires (D'Antonio and Vitousek 1992; Brooks et al. 2004). In a regularly burnt ecosystem, such as in East African savannahs, understanding the relationship between an individual alien species and fire is key to controlling and managing the growth and establishment of the species.

The Serengeti National Park is an internationally iconic protected area that receives several hundred thousand visitors annually (TANAPA 2017). As part of wildlife policy in Tanzania, the Park is considered a "pristine" or "semi-pristine" environment designated for the protection of its ecological integrity, thus prohibiting any introduction of alien flora and fauna (MNRT 1998). In spite of its iconic status, little work has been done to document the occurrence and identify sources and the impact of management on alien plant species in the Park. In this study, we aimed to (1) establish a list of alien plants in the Serengeti; (2) quantify the frequency of alien plant species near potential primary sources, i.e. roads and tourist settlements, around the park, and (3) estimate the abundance (plant cover) of alien plant species in relation to source activities (i.e. gardening, building and construction, road maintenance, garbage dumping, and settlement) and park management (i.e. fire). This information will help inform park management authorities of priority areas at risk of invasion as well as the impact of current habitat management on the occurrence and spread of alien plant species.

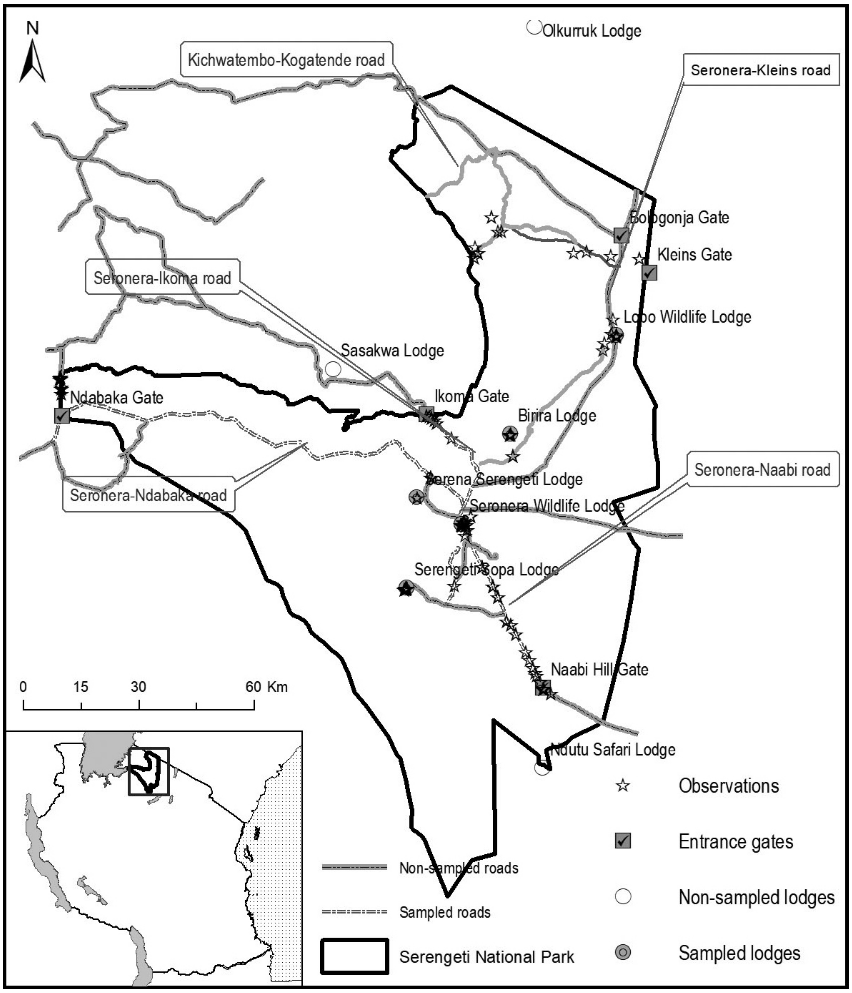

Figure 1. Locations of surveyed transects across main roads and settlements inside Serengeti National Park in 2013.

Methods

Study area

The study was conducted in the Serengeti National Park, northeast Tanzania, between latitude 2º and 2º30″S and longitude 34º and 34º30″E (Figure 1). Serengeti National Park is in the central part of the Serengeti ecosystem, covering an area of 14,700 km^2. Elevation in the Serengeti ranges from 920 to 1850 m a.s.l. Rainfall is seasonal, with a distinct dry season from June to October with typically < 50 mm of rain, and a wet season between November and May with around 1200 mm of rain (Krebs 1999). There is a rainfall gradient with increasing precipitation from wettest region in the west near Lake Victoria, receiving > 1000 mm annually, to driest in the shadow of the Ngorongoro Crater in the south-east plains with a rainfall of < 450 mm annually. Mean monthly maximum temperature averages between 27 and 28 °C all year round with a mean monthly minimum temperature between 13 and 16 °C (Sternberg et al. 2000). Underlying soil types are deep organic plansols and stagnosols in the west and shallow leptisols in the south east (IWG-WRB 2007). The predominant vegetation in the south is short and long grass plains with the central extensive block of the Park characterized by *Acacia* savannah woodland. The western corridor is dominated by wooded highlands and a concentration of wooded grassland is found around tributaries of Grumeti and Mara rivers. In general, the Serengeti woodlands are mainly composed of *Acacia*, *Balanites* and *Commiphora* species with other broad leaved species such as *Terminalia*, *Euclea* and *Croton* as sub-dominates in some region (Rao and Girish 2007). The park is managed regularly by burning (Stronach 1989), with higher frequencies (i.e. shorter intervals between fires) in wetter regions to the west and lower frequencies in the drier east.

Fire management is concentrated at the end of the short-wet season (March) and again at the end of the long-wet season (June–July) (Sinclair and Norton-Griffiths 1995; TANAPA 2017) to reduce risk of uncontrollable or damaging fires later in the dry season.

The Park contains high diversity of ungulates, large carnivores and birds, particularly one of the largest animal migrations by Wildebeest (*Connochaetes gnou* Zimmermann, 1780) (Sinclair and Norton-Griffiths 1995; Bukombe et al. 2015). Together these contribute to making the park a UNESCO heritage site and this is the main attraction to tourist visiting protected area in Tanzania. To accommodate tourists there are 10 lodges and 32 tented camps, totalling 56 accommodation sites (TANAPA 2017). When in the Park, tourists spend approximately 40% of their time in lodges and/or 43% in tented camps (Eagles and Wade 2006). All wildlife tourism is conducted from vehicles inside the Serengeti National Park, because tourists are not permitted to leave their vehicles except within the boundaries of gates and accommodation. Around the Serengeti National Park there is approximately 2160 km of gravel roads (estimate adapted from data used in Hopcraft et al. 2015). This infrastructure across the park is used by tourists, but also for socio-economic purposes with goods and people being ferried from population centers around Mwanza and Musoma in the west near Lake Victoria to Arusha in the east and vice versa (Figure 1). Indeed, preliminary plans to pave the Serengeti road and improve the connections outside the park between the west and east has raised international controversy for potential negative impacts on wildlife (see Hopcraft et al. 2015), although there has been limited discussion on the potential impact for introducing alien species. In the Serengeti National Park, roads traversing the Park serve as corridors, which connect weed populations in adjacent areas with the interior protected area (Figure 1). Road grading and road improvements may contribute to the recruitment of alien plant species in the Park.

Field surveying and ancillary data

In this work we considered an alien plant species as any plant species not native to Tanzania according to the Tanzania Biodiversity Information Facility (TanBIF 2010). Species were defined as alien by reference to a history of invasion within the country or elsewhere in East Africa (ISAC 2006). We recorded all alien plants, including those that had been naturalized. A naturalized alien plant species is one which establishes new self-perpetuating populations, undergoes widespread dispersal and becomes incorporated within the resident flora, whereby various barriers to regular reproduction have been overcome (Richardson et al. 2000).

All data collection took place in December 2013 to coincide with peak flowering during the short wet season and ensure the highest chance of species identification. Roads were sampled in the four main regions of the Serengeti National Park: Central (road section within Seronera area 20 km), North (the road section from Lobo through Kleins, Kichwatembo to Kogatende and TaboraB gate 200 km), West (the road from Musabi through Ndabaka Gate to Robana bridge 150 km) and South (the road section from Hippo pool through Naabi to Olduvai river 40 km) (Figure 1). We surveyed a total of 410 km, or approximately 20%, of all gravel roads found in the Serengeti. Line transects were established along each road section (Gelbard and Belnap 2003), and sampling occurred approximately every 8 km, totalling 52 sample locations. Transects avoided Kjøpes (large rocky mounds), lakes, swamps and major rivers. Transects started from the road center and continued perpendicular to the road for a distance of 200 meters. Presence or absence of each alien plant species was recorded within every 50 m section of transects. For each first encounter of an alien species along the 200 m transect, total alien plant species cover was recorded within a 5 m × 5 m quadrat. We sampled six settlements, five lodges: Seronera, Sopa, Bilila, Serena Lobo lodges and a single campsite, Bush camp (Figure 1). Although this sample size is small compared to the total number of lodges and campsites in the Serengeti National Park, we selected only sites that have existed in the Park for longer than 5 years and where alien species are likely to have had sufficient time to establish and are thus likely source populations. At each settlement we surveyed 12 transect at random cardinal directions from the centre of the settlement, totalling 72 transects, following a similar protocol as road transects outlined above. The location of the start and end of all transects as well as the site of first-encounter quadrat were recorded using a GPS. In total there were 124 surveyed 200 m transects across both roads and around settlements.

To provide further information as to the possible underlying reason for the establishment of the alien plant species, for each first encounter quadrat with an alien species we classified the "source activity" into six categories: construction site, garden, road maintenance (i.e. rubble from remedying defects and guttering drainage ditches near roads), settlement (i.e. near housing, stores, toilets etc.) and designated waste dumping (i.e. rubbish). Alien plants encountered at a single plant or patches at any locality were therefore considered as an independent observation in relation to their habitat. In total, there were 104 sampling points with a description of source activity across both roads and around settlements.

Fire frequency of the all first-encounter quadrat sampling locations were obtained from MODIS Burned Area Product from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS MCD 45A) with a pixel resolution of 500 m × 500 m (Roy et al. 2008). For each quadrat location, fire was recorded for each year between 2000 and 2013 as either zero or one, where zero was no fire and one was at least one fire occurrence. January through March 2000 was not included as the MODIS burn area product was only available from 1st April 2000. Additionally June 2001 was excluded from our analyses due to a satellite technical failure. The cumulative fire raster layer and vector shapefile of quadrat spatial locations were then intersected to obtain fire frequency over the 13 year period for each first-encounter quadrat in R version 3.3.1 (R Foundation for Statistical Computing 2016).

Data analysis

To evaluate the prevalence of alien plants in the Serengeti National Park we estimated probabilities of the presence versus absence of alien plant species near roads and settlements. For the main analysis, we compared presence versus absence of alien species for all our 200 m transect surveys using a generalized linear mixed model following a Bernoulli distribution with logit transformation. Fixed factors in the model included: source (i.e. settlement or road), distance from the source, using the four sub-divisions of the transects; 0–50 m, 50–100 m, 100–150 m and 150–200 m, alien plant species identity and cumulative fire frequency. The random components of the model were "area" (i.e. regions within the Serengeti) and transect identity to account for the nested design of 50 m transects sub-sections within the larger transect. Due to model convergence problems when including species with very low occurrences, only species that had total frequencies greater than 1.5% were included in the analysis, thus totalling 8 alien plant species (Table 1). The model was simplified based on the lowest Akaike Information Criterion (AIC) scores when comparing models with and without covariates (Zuur et al. 2009; Hilbe 2011). The final model was validated: firstly by checking for over-dispersion of residuals, and secondly, by simulating 10,000 datasets based on the model coefficients and comparing the frequency of simulated and observed data for presence and absence of alien species. In our final model residuals were not over dispersed with a ratio of 0.96 of the residual deviance divided by residual degrees of freedom and with a good fit between simulated data and observed data on presence of alien plant species, yet it slightly underestimated the absence of alien plant species. Given the large sample size of the dataset (496 observations; 124 transects × 4 distance sub-divisions), significance of factors was determined using likelihood ratio test (LRT) contrasting models with and without the fixed factor to generate p-values (Bolker et al. 2009). All analyses were carried out in R version 3.3.1 (R Core Team. 2016) with generalized mixed models tested using the "glmer" function in lme4 package R.

The abundance of alien plant species in relation to source activities, fire frequency and alien plant species identity was tested using a generalized linear model following gamma distribution (positive cover values) with log transformation. Initially we implemented data analyses using a generalized mixed model similar to the one outlined above, but we encountered significant issues with spatial autocorrelation for first encounter quadrat data that was not accounted for by the random components in the model. Therefore we adopted a Bayesian approach using a generalized linear model but with a spatial dependency structure in the model using the R-INLA package in R (Rue et al. 2009). In this model we used diffused priors, as we assumed no prior knowledge of the size of coefficients for each covariate. To account for the spatial distribution, latitude and longitude were used as part of a matérn correlation matrix incorporated into the model via a stochastic partial differential equation (SPDE) (Lindgren et al. 2011). The model was validated visually by comparing overall residuals versus fitted values and residual in comparison to covariates as well as simulating the predicted values from the model. The final model was selected based upon Watanabe-Akaike Information Criterion (WAIC) scores derived from contrasting models with and without covariates and the SPDE component (Zuur et al. 2009; Militino 2010). The importance of covariates in the final model was defined by the distribution of the posterior mean differing from zero (Supplementary material Figure S1).

Results

Presence of alien plant species near roads and settlements

Across 496 transect sub-sections in the Serengeti National Park we encountered 15 alien plant species (Table 1; Supplementary material Table S1). Of these species only 12 species occurred in more than 1% of observations. In our models, species identity was not a significant predictor of finding an alien species across our surveyed transects.

Table 1. Occurrence frequency and mean plant cover of first encounter quadrats (%) for alien plants found in Serengeti National Park. Percentage occurrence on roads, settlements and total (average) has been determined from the number of observations of a given species divided by number of transect section surveyed (i.e. for total occurrence 496 surveyed 50 m transect sections).

Common name	Scientific name	Family	Percentage occurrence			Mean plant cover– first encounter quadrat (%)
			Road	Settlement	Total	
Henequen	*Agave fourcroydes* Lemaire, 1864	Asparagaceae	0	0.4	0.2	1.0
Sisal	*Agave sisalana* Perrine, 1838	Asparagaceae	0	0.7	0.4	25.5
Blue agave	*Agave tequilana* F. A. C. Weber, 1902	Asparagaceae	0	3.5	2.0	45.6
Female finger	*Amaranthus hybridus* var. *hybridus* L, 1753	Amaranthaceae	8.1	3.8	5.6	44.8
Mexican Prickly poppy	*Argemone mexicana* L, 1753	Papaveraceae	2.8	0	1.2	54.0
Blackjack	*Bidens pilosa* L, 1753	Asteraceae	7.7	3.8	5.4	44.3
Coffee senna	*Cassia occidentalis* L, 1753	Fabaceae	1.9	0.7	1.2	57.5
Siam weed	*Chromolaena odorata* (L.) King & H.E. Robins, 1950	Asteraceae	3.4	0	1.4	23.7
Thorn apple	*Datura stramonium* L, 1753	Solanaceae	13.0	5.9	8.9	29.9
Upland cotton	*Gossypium hirsutum* L, 1763	Malvaceae	1.0	0	0.4	57.5
Tickberry	*Lantana camara* L, 1753	Verbenaceae	1.9	1.0	1.0	55.0
Prickly pear cactus	*Opuntia ficus-indica* (L.) Mill, 1753	Cactaceae	6.3	7.6	7.1	44.7
Castorbean	*Ricinus communis var.africanus* L, 1753	Euphorbiaceae	1.0	5.9	3.8	41.3
Stinking Roger	*Tagetes minuta* L, 1753	Asteraceae	17.3	10.4	13.3	39.9
Rough cocklebur	*Xanthium strumarium* L, 1753	Asteraceae	2.9	1.0	1.8	41.4

Nevertheless, species differ in their observed total frequency and the most encountered alien plant species were *Tagetes minuta* Linnaeus, 1753 (13.3%), *Datura stramonium* Linnaeus, 1753 (8.9%) and *Opuntia ficus* (L.) Mill, 1753 (7.1%) (percentages are as a function of total observations in all 50 m transect sub-sections; Table 1). Although, these occurrences are low, some of these species are notorious and problematic invasive; for example, *Chromolaena odorata* (L.) King and H.E. Robins, 1950 (Siam weed) was found in along the road near Robana bridge, west Serengeti.

We found that in the Serengeti National Park there is almost an 80% chance of encountering an alien plant species within the first 50 m from a road or settlement (Figure 2). Presence of alien plant species significantly declined with distance from roads and settlements (simplified generalized linear mixed model: Chisq = 363.3, df = 3, $p < 0.001$). Moreover, even at 200 m the probability finding an alien plant species was significantly higher than zero (Figure 2). For the most frequently encountered species, *Tagetes minuta*, *Datura stramonium* and *Opuntia ficus*, had a 33.1%, 22.6% and 19.4% probability of being present in first 50 m transect section. At the same time, areas closer to settlements and roads had more alien species with an average of 6.5 species for roads and 6.8 species for settlements, but averaged 1.6 species and 1.5 species and between 150 to 200 m from road and settlement sources, respectively. For the final reduced model, the presence and absence of alien species did not significantly differ between roads and settlements (full generalized linear mixed model: Chisq = 1.0, df = 1, p = 0.329), across different alien species (Chisq = 5.8, df = 7, p = 0.559) and in relation to fire frequency (Chisq = 0.4, df = 1, p = 0.548) (Figure 2).

Abundance of alien plant species in relation to human activities

The abundance of alien plant species near roads and settlements averaged 44.3 ± 2.3 % (mean ± SE) plant cover (Table 1). Swards of *Gossypium hirsutum* Linnaeus, 1763 and *Cassia occidentalis* Linnaeus, 1753 typically occurred as dense patches with the highest plant cover both averaging 57.5%, closely followed by *Lanata camara* Linnaeus, 1753 with plant cover of 55.0% (Table 1). Due to the large variation across species, species identity was not an important determinant of alien plant cover (Supplementary material Figure S1). Average alien plant covered varied across source activities with the highest around gardens

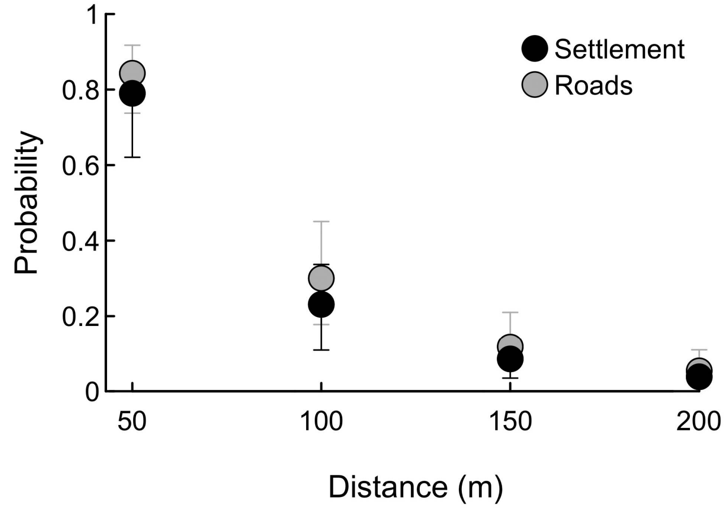

Figure 2. Probability of presence versus absence of an alien plant species in the Serengeti National Park at increasing distances away from roads (light grey symbols) and settlements (dark grey symbols). The probability has been derived from the odds ratio of a generalized linear mixed model with Bernoulli distribution. Road versus settlements was not included in the final simplified model. Error bars ± 1 SE.

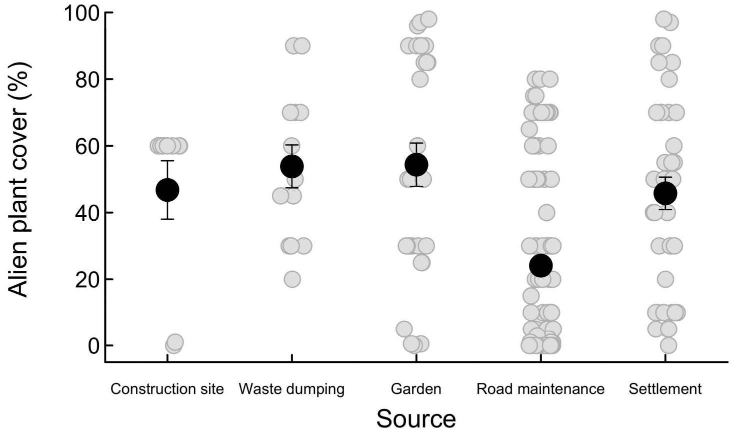

Figure 3. Total alien plant cover (%) in relation to human source activities in the Serengeti National Park, Tanzania. All surveyed quadrats are shown in light grey symbol and average source activity cover is shown as a black symbol. Error bars ± 1SE.

(54.4%), followed by waste dumping (53.8%), construction sites (46.8%), settlements (45.8%), and lowest around road maintenance areas (24.1%) (black symbols in Figure 3). However, overall source activities were not important for alien species plant cover with large variations across quadrats for each category (smaller grey symbols in Figure 3; Figure S1). However, alien plant species cover was highest in areas with the low cumulative frequency of fires (i.e. fewer fires) (Figure 4a). Areas without fires in the last 13 years had the highest predicted alien plant cover of 46.0%, while this declined to 16.4% plant cover for four fires over the same period. Although there were no differences in alien plant cover between roads and settlements, surveyed areas near to settlements had fewer fires with a median of one fire year between 2000 and 2013, while roads had a median of three fire years during the same time period (Figure 4b). Additionally, we detected species that had higher plant cover with more frequent fires, namely *Tagetes minuta* that dominated plots in areas with over eight fire years.

Discussion

Protected areas are the foundation of national and international conservation initiatives with a mandate to conserve biodiversity. The Serengeti National Park is a prime example of such initiatives, centred around protecting ungulates and mega-fauna (Sinclair 1995; Thirgood et al. 2004) and part of this mandate includes preventing the introduction of alien species (MNRT 1998). However, as this study highlights alien plant species are present throughout the Serengeti National Park, with an 80% probability of encountering an alien plant species within 50 m of a road or settlement (i.e. tourist lodge or campsite). Using a similar survey design, Witt et al. (2017) found 245 alien species in the Masai-Mara National Reserve, Kenya, which is adjacent to the Serengeti. In comparison, the prevalence of alien plant species in the Serengeti was much lower with only 15 species detected in our surveys. The reasons for this difference in species numbers may be due to reasons such as density of tourist numbers around settlements, infrastructure development, proximity and interactions with livestock as well as the intensity and duration of sampling. However, the underlying reason for such differences may equally relate to contrasting park fire management strategies. The Serengeti National Park typically has a higher fire frequency than the Masai-Mara National Reserve (Roy et al. 2008). In our study, we found that the absence of fire or extended periods without fire is positively related to alien plant species.

In this study, we aimed to make an inventory of alien plants in the Serengeti National Park. All alien plant species found in the Serengeti National Park have also been listed as invasive elsewhere in Africa. For example, *Amaranthus hybridus*, *Xanthium strumarium*, *Agave sisalana*, *A. americana*, *D. stramonium* and *Ricinus communis* are known invasive plants across South Africa (Hancock and Olivier 2017). Moreover, the alien species found in the Serengeti are common in agricultural areas in Tanzania (Sheil 1994; Jackson et al. 2008). Many of these species have toxic effects on livestock, and likely on wildlife, through alkaloids in seeds and other plant parts (for example, *C. odorata, D. stramonium* and *X. strumarium*) as well as allelopathic effects on surrounding native species (Weaver and McWilliams 1980; Butnariu 2012). Worryingly, we found some of the first records of *C. odorata* inside the Serengeti National Park near Robana bridge in this study. Recently we have observed this species also along Mbalageti River on western corridor and near bush camp in north (Bukombe, pers. comm.). *Chromolaena odorata* was first recorded in an area east of Lake Victoria between the Mara River and Kenyan border and has been spreading southwards, yet to date there has been no previous detection of this species inside the park (Shackleton et al. 2017). The species is typically a plant of secondary succession, which rapidly out-competes native species in grazing and drainage areas. Indeed, outside the Serengeti National Park some villagers are struggling to control this and other alien species on pastureland with the use of traditional methods such as slashing plants to ground level without removing rootstock or addressing seed dispersal. A coordinated approach, involving cooperation between park authorities and villagers outside the park is

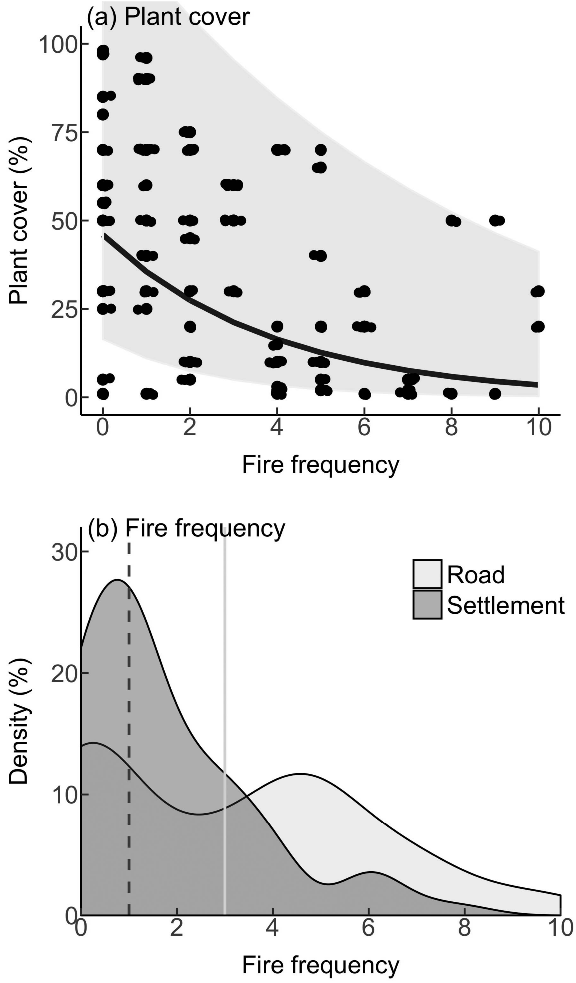

Figure 4. (a) Total alien species plant cover in relation to cumulative fire frequency from 2000 to 2013 and (b) the fire frequency as a percentage of total number of surveyed transects for roads (light grey) and settlements (dark grey). The line of best fit for plant cover is derived from a generalized linear mixed model using gamma distribution. Vertical lines on the histogram correspond to the median fire frequency for roads (solid light grey) and settlements (dashed black).

required to control these species. Additionally, management strategies need to account for different growth patterns and spread mechanism of these species (Javaid and Anjum 2006).

Understanding the sources that facilitate alien species invasion, establishment and spread in an ecosystem is key to their management and control. In our study we found no significant differences in the presence or plant cover of alien species in relation to settlements and roads. Furthermore, alien plant species presence and cover was unrelated to common source activities that have been previously shown to facilitate alien species introduction. Both findings are somewhat surprising given that Witt et al. (2017)

found settlements to be stronger hubs of alien species in comparison to roads in the Masai-Mara ecosystem. Again in the nearby Ngorongoro Conservation Area, east of the Serengeti, construction sites following buildings, road maintenance and garbage dumping were identified as encouraging alien plant species recruitment (Foxcroft et al. 2006). However, neither study accounted for the impact of the fire regime on alien plant species. Across the Serengeti, both roads and settlements surveyed varied in their fire frequency and this may serve to blur potential differences between these sources (see Figure 4b).

As opposed to other pyrobiomes such as prairie grasslands (D'Antonio and Vitousek 1992; Brooks et al. 2004), the relationship between fire and many alien plant species in savannahs remains largely understudied (Masocha et al. 2011). In one of the few studies that have directly investigated the long-term impact of fire manipulation on alien species in Zimbabwe, increased fire frequency was positively related to the number and density of alien species (Masocha et al. 2011). However, we found the opposite effect that alien species cover increased with fewer fires or an absence of fire, but that fire frequency had no effect on the initial presence of an alien species. This difference in alien plant cover may be due to species-specific interactions with fire. Furthermore, in the fire manipulation study in Zimbabwe outlined above, Masocha et al. (2011) found all of the five alien species surveyed differed significantly in their abundance in relation to fire frequency. Two of these species are shared across our studies: (1) *Tagetes minuta* was found to be an exception in our study and was positively associated with more frequent fires and also was positively associated with fire frequency in Masocha et al. (2011), while (2) *Bidens pilosa* was non-significantly associated with frequent fires in Masocha et al. (2011) and in our study we found this species to have higher abundance with less frequent fires. Although this work is limited, our studies suggest strong species-specific relationships between alien species in African savannahs and fire frequency as seen in other pyrobiomes (Brooks et al. 2004). However, such species-specific relations with fire will make alien species management using fire challenging. Despite the majority of species being negatively associated with fire in the Serengeti, enhancing fire frequencies in dense alien species areas will select for species promoted by fire such as *Tagetes minuta*. Additionally, increasing fire frequencies will strong implications on other properties of the savannah ecosystem, such as altering the composition, productivity and abundance of native woody species as well as impacts on other ecosystem functions such soil nutrient availability and carbon (Higgins et al. 2007; Bond and Midgley 2012). Moreover, promoting fire frequency in close proximity to lodges will present a human health and structural risk. Therefore other interventions such as biological control agents would be necessary to remove alien species, but their use should also consider possible interactions with fire.

Now established, the 15 alien plant species identified in the Serengeti National Park will be difficult to eradicate from the ecosystem. A growing body of research advocates the use of biological control agents (i.e. insect herbivores or pathogens) to manage alien plant species in East African protected areas (Shackleton et al. 2017; Witt et al. 2017). In these studies there are many successful examples using biological agents to control problematic alien invasive species across Africa. In spite of the success of such agents, their use needs to be investigated in combination with common management strategies in protected areas, namely fire. These authors also raise the importance of cooperation between East African authorities' of protected areas in monitoring and managing alien species. Provided sufficient further research, our study extends this cooperative gesture further to coordinate fire management strategies in order to control the abundance of alien plant species. Equally, park authorities also need to cooperate with villagers outside the protected areas (Shackleton et al. 2017). The majority of alien species found in the Serengeti are common alien species in Tanzanian agricultural land. Public awareness (Wittenberg and Cock 2001) and support (Bragg and Hulbert 1976) will be necessary components of controlling and managing alien species in East African protected areas.

Acknowledgements

We thank Serengeti National Park for funding this work. We are grateful to Andrew Kittle and Susanna Karlsson for comments on earlier versions of this manuscript. Thanks to Dr. Robert Fyumagwa, Director of the Serengeti Wildlife Research Center for facilitating the occurrence of field works. JB, HZ, EK were funded by the Serengeti National Park and SWS was funded by EU2020 AfricanBioService (grant number 641918).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Identification photographs of alien species found within the Serengeti National Park, Tanzania.

Figure S1. Posterior mean distributions for all covariate betas derived from the Bayesian generalized linear model with spatial dependency structure.

This material is available as part of online article from:

http://www.reabic.net/journals/mbi/2018/Supplements/MBI_2018_Bukombe_etal_Table_S1.pdf

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