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RESEARCH ARTICLE

Associations between *Lantana camara* L. (Verbenaceae) and common native species in an African savanna

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Abstract

1. *Lantana camara* L. (Verbenaceae) is recognised as a problematic invasive alien plant species in many parts of the world. To eradicate or control this global invader, we need to understand the drivers of its spread and impacts and the potential for native recovery after the invader has been removed.
2. Here, we tested for species associations between *L. camara* and native plant species and large herbivores in Queen Elizabeth National Park, Uganda. We inventoried 40,100-m^2 nested plots spread over a 1 × 1-km grid cell in the park's savanna landscape, with 11 plots located in uninvaded areas. Most of the plots (30 of 40) had been affected by fire.
3. *Lantana camara* covered 29 (73%) plots, 11 (38%) of which were in open grassland. Of the large herbivores that frequented areas free of *L. camara*, the Ugandan kob *Adenota kob thomasi* Sclater tended to avoid the areas invaded. The floristic composition of invaded areas differed significantly from that of noninvaded areas, with several palatable species rare or absent from *L. camara*-invaded areas.
4. *Practical implication*: These observations indicate the presence of potential recovery constraints that will need to be overcome after *L. camara* has been removed. Sustained efforts will be needed to suppress the invader and subsequently enrich and bolster native recovery.

KEYWORDS
abundance, grassland, invasive species, large herbivores, species composition, vegetation recovery

1 | INTRODUCTION

Invasive alien species are considered a threat to native biodiversity (Bellard et al., 2022; Chapman et al., 2022; IPBES, 2023). Alien species can alter ecosystem structure and functioning, as well as lead to biotic impoverishment and homogenization (Foxcroft et al., 2010; Stotz et al., 2019). Native species face a high risk of extinction, especially those that are rare and endangered, posing significant threats to agricultural food production, natural resource collection and human well-being (Boy & Witt, 2013; Olden, 2006; Shackleton et al., 2017). These impacts strongly affect local people, as they rely more on natural resources to meet their day-to-day needs (Eilu et al., 2003; Gumisiriza et al., 2019; Wild & Mutebi, 1996). Therefore, understanding how to deal with alien species that occur in protected areas (PA) is critical to reduce impact and enhance benefits given the key role of PA in the

conservation of biodiversity and the maintenance of ecological processes.

Invasive alien species have become widespread and occupy areas that are important for conservation (Kipkoech et al., 2020; Lusweti et al., 2011; Richardson et al., 2022). Such widespread invasions may be explained by a combination of species attributes (invasiveness), multiple introductions (propagule pressure) and environmental degradation (Kueffer, 2017; Simberloff, 2010; Witt et al., 2018). Notable among the widespread plant invaders considered problematic is *Lantana camara* L. This erect and hardy evergreen perennial shrub belonging to the Verbenaceae family originates from Central and South America (Fischer et al., 2010; Germishuizen & Meyer, 2003; Kipkoech et al., 2020). It grows best in open, unshaded environments where there is more light availability (Carrión-Tacuri et al., 2011; Day & Zalucki, 2009; Duggin & Gentle, 1998). The invasive shrub tends to recover from fire faster than native species and becomes dominant in frequently burned areas (Day & Zalucki, 2009; Safari & Byarugaba, 2008).

Lantana camara forms dense thickets that have a range of negative impacts including poisoning animals, suppressing native forage species, obstructing access to water sources and degrading rangelands (Day & Zalucki, 2009; Hamad et al., 2022; Ntalo et al., 2022; Wronski et al., 2017). *L. camara* thickets reduce the available nutrients, light and space and may hinder the growth of other plants through the release of allelopathic chemicals (Gentle & Duggin, 1998; Wekhanya et al., 2020). This invasive species is hard to eradicate, as it flowers and fruits throughout the year and is readily dispersed by many native bird species (Totland et al., 2005). It also reproduces vegetatively and has a persistent seed bank (Bitani & Downs, 2022; Totland et al., 2005). The invader can be brought under control by integrating various mechanical, biological, chemical and land management techniques into conservation practice (Bhagwat et al., 2012; Simelane et al., 2021). For example, people may harvest the plant regularly until it is eliminated (Kannan et al., 2014). Knowledge of the factors that contribute to *L. camara* invasiveness offers an improved understanding of the management strategies needed to minimise its spread and impacts.

To explore associations between *L. camara* and common native species, we set up a study across 40 inventory plots located in invaded and uninvaded areas in Queen Elizabeth National Park. Specifically, we asked: (1) whether floristic composition varies between *L. camara*-invaded and uninvaded areas and (2) which large herbivores forage in areas with *L. camara*. Answers to these questions will help guide the management and restoration initiatives that will be undertaken after *L. camara* has been removed. This study is part of a long-term vegetation monitoring programme which aims to investigate the different techniques, methods and approaches for eradicating invasive plant species from the park.

1.1 | Study area

The study was conducted in Queen Elizabeth National Park in July 2021. The 1978 km^2 park (hereafter 'QENP') is located in the western Rift Valley of Uganda near the Rwenzori mountains and is between two freshwater lakes (that is, Lakes Edward and George) linked by the Kazinga channel (Figure 1; Braczkowski et al., 2020; Lock, 1972; Plumptre et al., 2007). The climate is equatorial with two rainfall peaks from March to May and September to November (Chritz et al., 2016). The driest months are December–February and July–August. Temperature fluctuations are minor and oscillate between 16°C in March and 27°C in January. The park comprises a range of habitat types, including grasslands, woodlands, wooded grasslands, bush/scrub, Euphorbs, papyrus swamp, riverine forest and tropical high forest (Plumptre et al., 2010; Uganda Wildlife Authority, 2012). Common species include woody plants *Acacia sieberiana* DC., *Acacia gerradii* Benth. and *Acacia hockii* De Wild., graminoids *Hyparrhenia filipendula* (Hochst.) Stapf, *Themeda triandra* Forssk., *Imperata cylindrica cylindrica* (L.) Raeuschel and *Cymbopogon afronardus* Stapf, and a large number of forb species, including many legumes (Lock, 1993). *Lantana camara* is locally abundant, occurring over 66 km^2 of the park (Plumptre et al., 2010). It is spreading and has been identified as a species of management concern (Solberg, 2022; Uganda Wildlife Authority, 2012).

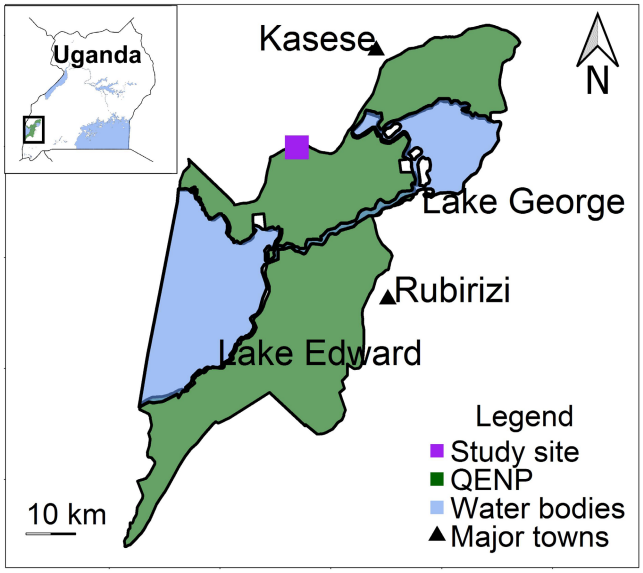

FIGURE 1 The location of *Lantana camara* study plots in a savanna landscape in Queen Elizabeth National Park, Uganda.

2 | MATERIALS AND METHODS

We inventoried 40 nested plots spread over a 1×1-km grid cell (Appendix 1) and recorded woody species within 10×10-m plots, forbs within 5×5-m plots and graminoids within 1×1-m plots. Each nested plot comprised the 10×10-m plot, one 5×5-m plot and one 1×1-m plot, with the smaller plots located at the centre of the main plot. Plot centres were predetermined using QGIS, assigned unique plot numbers and located for on the ground using a GPS. Each inventory plot was visually examined for evidence of past fire

and classified as 'frequently burnt' or 'rarely burnt' if the burning occurred during the two dry seasons each year or not, respectively. To determine which large herbivores forage in *L. camara*-invaded areas, we sought and examined evidence of herbivore activity including animal trails, footmarks, droppings and browsing damage. We used the presence and absence of animal signs per plot to calculate the percentage of large herbivores that utilise these areas and tested for differences in herbivore activity using negative binomial GLM. The glm.nb function from the R 'MASS' package was used to perform the GLM analysis (Venables & Ripley, 2002).

The invasion of *Lantana camara* was evaluated in 10×10-m plots and classified into two classes using the 75th percentile as a threshold: 'uninvaded' (*Lantana* density = 0) and 'invaded' (*Lantana* density ≥ 0.25 stems m^{-2}). To determine whether floristic composition varies between invaded and uninvaded areas, we summarised, plotted and analysed the data using R (R Core Team, 2020). We summarised species diversity patterns using Fisher's diversity index and tested for differences in *L. camara* invasion between vegetation types (that is, open grassland versus wooded grassland) and burning regimes (that is, 'frequently burnt' versus 'rarely burnt') using Mann Whitney tests. We determined whether inventory plots were spread along a gradient from lower to higher levels of *L. camara* invasion by performing non-metric multidimensional scaling (NMDS) ordination using the community ecology package 'vegan' (Oksanen et al., 2020). Kendall rank correlations between ordination axes and the relative abundance of *L. camara* were calculated to aid interpretation. Species abundance data for the plots were transformed into $\log_{10}(x+1)$ to minimise the influence of the most abundant species, and Bray–Curtis dissimilarities were calculated (Bray & Curtis, 1957; Oksanen et al., 2020). One-way analysis of similarities (ANOSIM) was performed to determine whether there were significant differences in species composition between paired invaded and uninvaded plots.

3 | RESULTS

Of the 40 plots inventoried, 29 were located in open grassland and the other 11 in wooded grassland. Based on site history, 30 plots were frequently burnt, while the remaining 10 were rarely burnt (Table 1). *Lantana camara* was present in 29 (73%) plots, 11 (38%) of which had 25 or more *L. camara* stems per plot of 100 m^2. The number of *L. camara* stems per plot ranged from 0 to 350. The relative abundance of the invader ranged from 0 to 70.9, with the latter recorded in a plot containing four woody species *Acacia gerradii*, *Grewia similis*, *Flueggea virosa and Capparis tomentosa* (Table 1; Appendix 2). We recorded a total of 84 plant species (including *L. camara*), comprising 21 graminoid species, 44 forb species and 19 woody plant species (Appendix 2). The plant species belonged to 27 families, with Poaceae ($n = 17$ species), Euphorbiaceae ($n = 6$), Asteraceae ($n = 5$), Fabaceae ($n = 5$), Lamiaceae ($n = 5$) and Malvaceae ($n = 5$) containing the most species (Appendix 2). The plots on open grassland exhibited a significantly lower abundance of *L. camara* than those on wooded grassland (mean ± 1 SE: 5.4 ± 1.4 vs. 30.5 ± 2.6; Mann Whitney test, $W = 300.5$, $p < 0.001$). Other relationships between *L. camara* abundance, Fisher's alpha, vegetation type and burning regime were not significant (see Figure 2). Large herbivores foraged in just over half (6 of 11) of the plots in *L. camara*-invaded areas and in nearly all (9 of 11) plots in uninvaded areas (Table 2). The African bush elephant *Loxodonta africana* Blumenbach generally ate more in invaded areas than uninvaded areas (36% vs. 9%), although this was not significant (negative binomial GLM $\chi^2 = 1.93$, $p = 0.165$) while the Uganda kob *Adenota kob thomasi* Sclater were significantly more common in uninvaded areas (9% vs. 54%, negative binomial GLM $\chi^2 = 3.96$, $p = 0.047$, see Table 2).

Across 11 *L. camara*-invaded plots, 53 plant species comprising 14 graminoids, 26 forbs and 13 woody species were recorded. In contrast, 47 plant species comprising 16 graminoids, 17 forbs and 14 woody species were recorded across 11 uninvaded plots (Appendix 2; Figure 3). Thirty-three species including *Panicum maximum* Jacq., *Achyranthes aspera* L. and *Acacia gerradii* Benth. were common in invaded and uninvaded plots, while 19 species including *Setaria kagerensis* Mez, *Bidens pilosa* L. and *Olea europaea* subsp. *africana* L. were found only in invaded plots and 14 species including *Themeda triandra* Forssk., *Brachiaria platynota* (K.Schum.) Robyns and *Cymbopogon afronardus* Stapf occurred only in uninvaded plots (Table 3; Appendix 2). The three most abundant species that occurred in invaded plots were the perennial forb *Acalypha bipartita* Muell. Arg. ($n = 320$), followed by perennial grass species *P. maximum* ($n = 107$) and *Chloris gayana* Kunth ($n = 99$). In the uninvaded plots, *P. maximum* ($n = 66$) was the most abundant species followed by *C. gayana* ($n = 62$) while *A. bipartita* ($n = 59$) ranked third (Table 3 and Figure 3).

Pairwise comparison of the floristic dissimilarity ranked between invaded and uninvaded areas revealed significant differences in the composition of graminoid and woody species (ANOSIM; $p < 0.05$; Appendix 3). The NMDS ordination showed a clear separation of inventory plots in invaded areas from those in uninvaded areas, suggesting that *L. camara* invasion may explain the observed floristic dissimilarity (Figure 4). Furthermore, the first axis of NMDS ordination was positively correlated with relative abundance of *L. camara* (Kendall rank correlation, $\tau = 0.53$, $n = 22$, $p = 0.001$), but the correlation of the second axis, although positive, was not significant ($\tau = 0.32$, $n = 22$, $p = 0.053$).

4 | DISCUSSION

Our study evaluated the ecological associations of *L. camara* and the potential effects of the widespread occurrence of the invader in an East African savanna park. The composition of both graminoid and woody species differed significantly between invaded and uninvaded plots, with three of 10 common graminoids and all but one of 10 common woody species occurring more commonly in invaded than in uninvaded areas (Table 3; Appendix 3). The three common graminoids (that is, *Sporobolus africanus* (Poir.) Robyns & Tournay,

TABLE 1 Characteristics of floristic inventory plots located in *Lantana camara*-invaded and uninvaded areas in QENP.

Plot ID	Habitat type	Burning frequency	Relative abundance of *L. camara* (%)	N graminoid species	N forb species	N woody species	Total N species	Fisher's alpha
1	Open grassland	More frequent	0	5	8	4	17	6.5
2	Wooded grassland	More frequent	15.6	2	10	10	22	6.4
3	Wooded grassland	Rare	16.1	1	6	10	17	6.0
4	Open grassland	Rare	3.1	6	13	7	26	12.0
5	Open grassland	Rare	31.7	4	7	6	17	6.1
6	Open grassland	More frequent	16.1	6	11	8	25	10.3
7	Wooded grassland	Rare	19.1	5	8	9	22	7.9
8	Open grassland	More frequent	1.3	3	10	6	19	8.1
9	Open grassland	More frequent	0	2	9	5	16	6.6
10	Open grassland	More frequent	0	5	7	8	20	11.0
11	Wooded grassland	More frequent	30.6	5	8	6	19	4.2
12	Open grassland	Rare	0	7	6	2	15	5.0
13	Open grassland	Rare	1.1	10	5	4	19	7.4
14	Wooded grassland	Rare	14.0	3	10	7	20	6.0
15	Open grassland	More frequent	0	5	9	2	16	6.9
16	Wooded grassland	More frequent	25.4	2	10	10	22	6.6
17	Open grassland	More frequent	9.2	2	12	7	21	8.5
18	Open grassland	More frequent	29.2	2	7	7	16	5.5
19	Open grassland	Rare	1.5	8	7	5	20	6.7
20	Open grassland	Rare	4.1	4	11	2	17	7.9
21	Open grassland	More frequent	0	9	5	2	16	5.2
22	Open grassland	More frequent	2.5	6	6	3	15	4.6
23	Wooded grassland	More frequent	31.0	2	13	6	21	7.4
24	Open grassland	More frequent	0	5	6	3	14	5.4
25	Open grassland	More frequent	1.4	5	7	3	15	5.5
26	Open grassland	More frequent	0	3	5	3	11	4.2
27	Open grassland	More frequent	0	5	4	3	12	4.6
28	Open grassland	More frequent	0.6	8	5	3	16	4.4
29	Wooded grassland	More frequent	39.5	1	6	3	10	2.8
30	Open grassland	More frequent	12.9	2	5	2	9	2.4
31	Open grassland	More frequent	18.8	5	9	5	19	7.1
32	Open grassland	More frequent	0	10	7	1	18	4.8
33	Wooded grassland	More frequent	31.5	3	8	8	19	6.8
34	Open grassland	More frequent	1.1	5	4	2	11	3.2
35	Open grassland	More frequent	10	4	8	3	15	5.5
36	Open grassland	More frequent	2.2	5	7	5	17	5.7
37	Wooded grassland	More frequent	42.0	6	3	5	14	3.4
38	Wooded grassland	Rare	70.9	2	11	5	18	3.8
39	Open grassland	More frequent	9.0	4	13	4	21	6.2
40	Open grassland	More frequent	0	6	3	1	10	3.6

Setaria spp. and *Cyperus rotundus* L.) occur in high-rainfall areas, where greater water availability likely allows these species to establish and spread into invaded areas and are known to be eaten by large herbivores (Field, 1970; Lock, 1972; Plumptre et al., 2010). Thus, *L. camara* may facilitate the growth of plant species that adapt to moist environments through reduced evapotranspiration and reduced herbivory, particularly along roadsides and in frequently burned and heavily grazed areas (Day & Zalucki, 2009; Petrides & Swank, 1965). However, the co-occurrence of *L. camara* with woody species is of particular concern, as it likely reflects the abundance

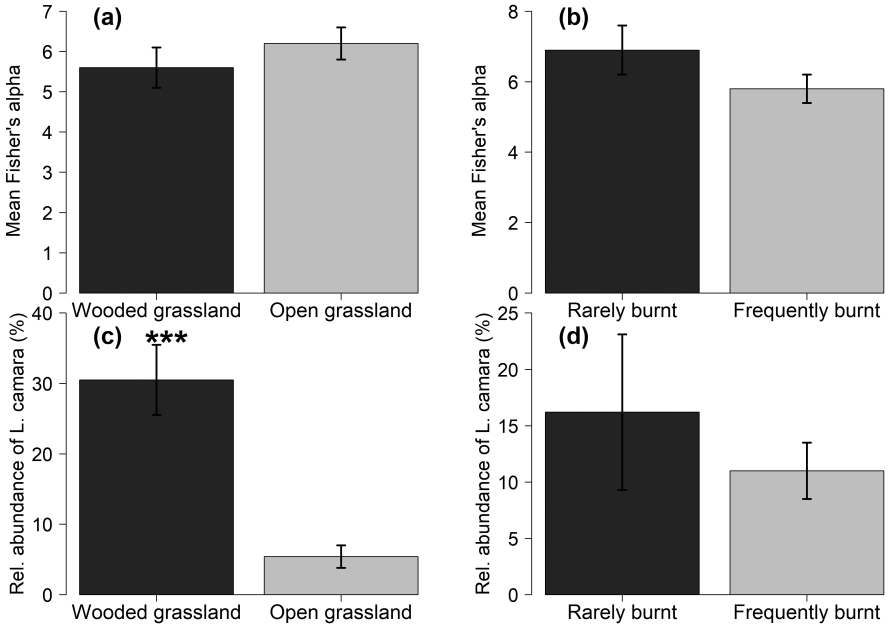

FIGURE 2 Fisher's alpha (a, b) and relative abundance of *Lantana camara* (c, d) versus vegetation type and burning regime in QENP. Significant differences are denoted by asterisks (Mann Whitney test, $p < 0.001$).

TABLE 2 Frequency (%) of large herbivores in *Lantana camara*-invaded and uninvaded areas.

Common name	Scientific name	Invaded	Uninvaded
African bush elephant	*Loxodonta africana* Blumenbach	36.4	9.1
African buffalo	*Syncerus caffer* Sparrman	54.5	54.5
Warthog	*Phacochoerus aethiopicus* Pallas	9.1	9.1
Uganda kob	*Adenota kob thomasi* Sclater	9.1	54.5
All large herbivores		54.5	81.8

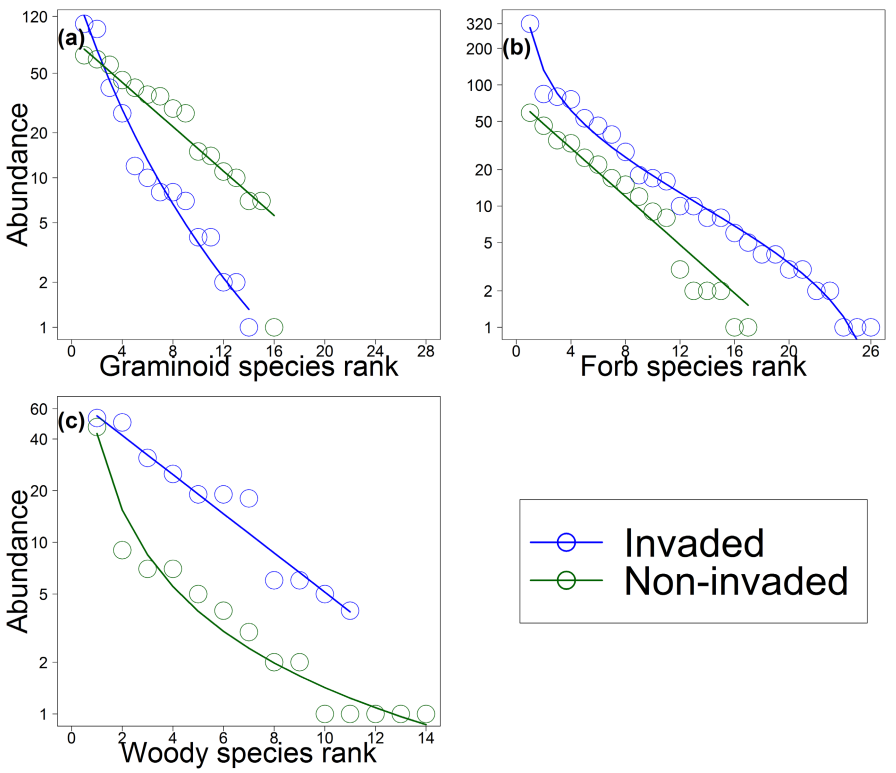

FIGURE 3 Rank abundance curves of (a) graminoids, (b) forbs and (c) woody species in *Lantana camara*-invaded and uninvaded areas. The models that provided the best fits for invaded and uninvaded areas, respectively, are as follows: (a) for graminoids, Zipf-Mandelbrot model versus niche pre-emption model; (b) forbs, log-normal model versus niche pre-emption model; and (c) woody species, niche pre-emption model versus Zipf-Mandelbrot model. The *x*-axis of each curve is the rank order of abundance, from most to least abundant, and the *y*-axis is the species abundance displayed on a $\log_{10}$ scale. See Appendix 2 for species rank identity.

TABLE 3 The density (stems $m^{-2} \pm 1$ SE) of the 10 most common graminoid, forb and woody plant species recorded in *Lantana camara*-invaded and uninvaded areas in QENP.

Family	Species	Invaded	Uninvaded
Graminoids			
Poaceae	*Panicum maximum* Jacq.	6.4 ± 1.6	6.0 ± 1.6
Poaceae	*Hyparrhenia filipendula* (Hochst.) Stapf	2.0	3.3 ± 1.8
Poaceae	*Sporobolus pyramidalis* P. Beauv.	1.0	2.8 ± 1.4
Poaceae	*Cynodon dactylon* (L.) Pers.	1.0	2.1 ± 0.8
Poaceae	*Sporobolus africanus* (Poir.) Robyns & Tournay	11.0	0.9 ± 0.8
Poaceae	*Setaria* spp.	12.5 ± 7.5	0.9 ± 0.7
Poaceae	*Themeda triandra* Forssk.	0	0.6 ± 0.4
Poaceae	*Cymbopogon afronardus* Stapf	0	0.5 ± 0.5
Poaceae	*Brachiaria platynota* (K.Schum.) Robyns	0	0.3 ± 0.3
Cyperaceae	*Cyperus rotundus* L.	0.2 ± 0.04	0.01 ± 0.03
Forbs			
Euphorbiaceae	*Acalypha bipartita* Muell. Arg.	1.4 ± 0.9	0.1 ± 0.07
Solanaceae	*Solanum incanum* L.	0.1	0.1 ± 0.06
Fabaceae	*Desmodium* spp.	0.1 ± 0.01	0.1 ± 0.06
Amaranthaceae	*Achyranthes aspera* L.	0.3 ± 0.1	0.1 ± 0.03
Vitaceae	*Cyphostemma adenocaule* (A. Rich.) Wild & Drumm.	0.1 ± 0.01	0.1 ± 0.02
Fabaceae	*Indigofera arrecta* A.Rich.	0.1	0.07 ± 0.04
Commelinaceae	*Commelina benghalensis* L.	0.2 ± 0.04	0.04 ± 0.03
Commelinaceae	*Commelina africana* L.	0.4 ± 0.1	0.02 ± 0.02
Lamiaceae	*Hoslundia opposita* Vahl	0.02 ± 0.004	0.01 ± 0.003
Malvaceae	*Abutilon guineense* (K.Schum.) Baker f. & Exell	0.5 ± 0.2	0
Woody species			
Fabaceae	*Acacia gerradii* Benth.	0.1 ± 0.002	0.04 ± 0.02
Asteraceae	*Vernonia* spp.	0	0.02 ± 0.01
Malvaceae	*Grewia similis* K.Schum.	0.1 ± 0.01	0.01 ± 0.004
Capparidaceae	*Maerua triphylla* (Thunb.) H.L.Wendl.	0.04 ± 0.01	0.01 ± 0.004
Phyllanthaceae	*Flueggea virosa* (Roxb. ex Willd.) Voigt	0.02 ± 0.004	0.01 ± 0.003
Anacardiaceae	*Rhus natalensis* Bernh.	0.04 ± 0.01	0.003 ± 0.001
Capparaceae	*Capparis tomentosa* Lam.	0.03 ± 0.01	0.002 ± 0.002
Ebenaceae	*Euclea schimperi* (A.DC.) Dandy	0.1 ± 0.03	0.001 ± 0.001
Euphorbiaceae	*Erythrococca trichogyne* (Müll.Arg.) Prain	0.04 ± 0.01	0.001 ± 0.001
Euphorbiaceae	*Euphorbia candelabrum* Kotschy	0.02 ± 0.01	0.001 ± 0.001

of the invader in areas where bush encroachment is widespread (O'Connor et al., 2014; Solberg, 2022). Studies in African savannas have shown that the co-occurrence of *L. camara* with woody species can be explained by the higher probability of bird dispersal and the invader's ability to tolerate moderate shade (Agaldo, 2019; McMahon & Ward, 2021; Rodger & Twine, 2002). It is likely that *L. camara* will spread to more areas in the park (RB, pers. obs.), hence the need to implement eradication or control measures.

Large herbivores tended to avoid areas with *L. camara*, as they were absent in five plots in invaded areas compared to two plots in uninvaded areas. The avoidance of *L. camara*-invaded areas was mainly exhibited by the Uganda kob, which frequently utilised areas without the invader (Table 2). This likely reflects the scarcity of food arising from grass decline, the susceptibility of falling prey to carnivores, and obstruction of animal movements in areas that are invaded (Day & Zalucki, 2009; O'Connor & van Wilgen, 2020). If large herbivores keep avoiding these areas, invasion by the alien *L. camara* will worsen due to reduced opportunities for recolonisation by herbivore-adapted species (Foxcroft et al., 2010; Standish et al., 2007). However, not all large herbivores were obstructed by *L. camara*, since megaherbivores (that is, elephants and buffaloes) were frequently observed in invaded areas (Table 2), although the invader likely modified their feeding rates, as has been observed for Asian elephant (*Elephas maximus*) in southern India (Wilson et al., 2014).

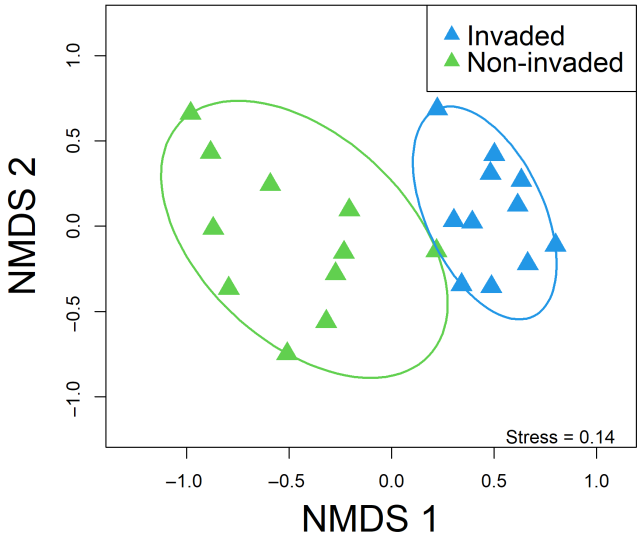

FIGURE 4 Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the species abundance data based on Bray–Curtis dissimilarities (Bray & Curtis, 1957) among *Lantana camara*-invaded ($n = 11$) and uninvaded ($n = 11$) plots. Ellipses are 95% confidence intervals of group centroids.

Thus, megaherbivores and possibly other terrestrial herbivores not recorded in this study (e.g. Hares *Lepus crawshayi*; see Ogen-Odoi & Dilworth, 1985) could explain the relatively high abundance of some of the common native plant species including *A. bipartita*, *P. maximum and C. gayana* in invaded areas (Table 3). More studies are needed to provide a deeper understanding of species interactions and factors that can promote or limit plant invasions, particularly in protected areas that must be kept free of alien species.

Species ranks and absences differed markedly between invaded and uninvaded areas, indicating that *L. camara* presence alters vegetation structure leading to lower abundance and diversity of native species (Appendix 2; Figure 3; see also Gooden et al., 2009). The highest-ranking species occurring in invaded areas, that is, *A. bipartita* (a scrambling subshrub <3 m), *P. maximum* (a large tufted perennial grass, up to 2 m tall) and *C. gayana* (a perennial grass forming tufts, 0.5 to 1.5 m tall), are known to be tolerant to shading and to various soil types (Fischer et al., 2010; Ludwig et al., 2008; Synnott, 1985) and thus may be able to persist over time after *L. camara* has been removed. These species were also common in uninvaded areas (Appendix 2). Park managers could use them as seed sources to promote rapid recovery. We also found that 14 of 84 species, including forage grasses *Themeda triandra* and *Brachiaria platynota*, known to be eaten by wild animals in QENP (Edroma, 1985; Petrides & Swank, 1965), occurred commonly in uninvaded areas, but were absent from invaded areas. This indicates that *L. camara* dominance leads to the exclusion of desirable species and is consistent with other studies that have shown that *L. camara* is an effective competitor against native species (Agaldo, 2019; Gentle & Duggin, 1998). Allelopathy and competition for resources including water, light and nutrients likely explain why these species are not able to establish and persist in invaded areas.

The richness of the forb species in invaded areas (26 species) was surprisingly higher than that in uninvaded areas (17 species) although there was considerable variation between observations (see Figure 3b and Appendices 2 and 3). In general, this finding may reflect the tendency of *L. camara* to prevent highly competitive grasses from dominating, which allows forbs to establish and persist in the face of recurrent disturbance caused by fire, grazing and trampling (Edroma, 1984). Forbs can tolerate a wider range of disturbance factors than dominant grasses, since many are unpalatable and have underground storage organs (Bråthen et al., 2021). The implication is that, in addition to resulting in severe bush encroachment (O'Connor et al., 2014; Plumptre et al., 2010), the widespread occurrence of *L. camara* could exacerbate the encroachment of non-graminoid herbaceous plants into the open grasslands of the park (see Chritz et al., 2016). Furthermore, a major invasive plant species *Dichrostachys cinerea* occurred in plots adjacent to the invaded areas with *L. camara* (Appendix 2). *D. cinerea* possesses several typical traits of successful invader species, including prolific fruiting, producing seeds capable of surviving for more than 5 years in the soil, and the formation of a canopy over other plants and suppressing their growth (Mudzengi et al., 2014). In QENP, there are some other invasive species including *Euphorbia candelabrum*, *Opuntia vulgaris and Parthenium hysterophorus* that are found within or near our inventory plots (Appendix 2; see also Nuwagira et al., 2020; Solberg, 2022). In our data set, 7 (8%) of the taxa recorded were alien species and two of these (i.e. *Alternanthera pungens* Kunth and *B. pilosa*) occurred more commonly in invaded than in noninvaded areas (Appendix 2). Therefore, we advocate restoration interventions aimed at controlling a broad suite of invaders that may come in after the eradication or decline of *L. camara*. More replicates are needed in future work to experimentally determine the impact of *L. camara* on native communities.

5 | CONCLUSIONS

The composition of graminoid and woody species differed significantly among invaded and noninvaded plots, with some palatable species virtually absent from invaded areas. Large herbivores, with the exception of megaherbivores, foraged in *L. camara*-invaded areas only occasionally, indicating an aversion towards a floristically impoverished area dominated by unpalatable plant species. In the face of recurrent disturbances, the abundance and spread of *L. camara* will likely increase and predispose larger areas to declines in palatable species diversity and increased bush encroachment. Management should focus efforts to suppress this invader.

AUTHOR CONTRIBUTIONS

Moses Muhumuza, Gilbert Drileyo and Robert Baluku planned and conducted the study. Fredrick Ssali analysed the data and wrote the first draft; Moses Muhumuza, Gilbert Drileyo and Robert Baluku reviewed and edited the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to disclose.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.c59zw3rhm (Ssali et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix 1. The 40 *Lantana camara* inventory plots spread over a 1 × 1-km grid cell in a savanna landscape in QENP.

Appendix 2. List of plant species recorded in *Lantana camara* invaded ($n = 11$), uninvaded ($n = 11$) and all plots ($n = 40$) inventoried in QENP.

Appendix 3. Pairwise comparison of ranked floristic dissimilarity between (a) graminoids, (b) forbs and (c) woody species recorded in *Lantana camara* invaded and uninvaded areas.

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