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Drivers and Ecological Impacts of Invasive Plant Species on Elephant Forage in Mwea National Reserve Kenya

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Abstract

Studies of the ecological impacts of invasive plant species on food availability for endangered species remain limited in invasion ecology. In this study, we used purposeful sampling and established ecological equations to assess the impacts of invasive plants on elephant food resources in Mwea National Reserve, an enclosed conservation area. A total of 85 randomly distributed plots (5 m × 5 m) were established across purposively selected invaded habitat types and used to quantify the drivers and ecological impacts of invasive plant species. We hypothesized that increases in the distribution, cover, and density of invasive plant species would reduce the abundance and availability of elephant forage plants in invaded compared to non-invaded sites. We documented a total of 11 invasive species, with *Parthenium hysterophorus*, *Senna didymobotrya*, *Xanthium strumarium*, and *Senna longiracemosa* exerting the strongest negative effects on native plant cover, an indication of their competitive dominance. In contrast, *Megathyrsus maximus* showed a positive association with native cover, suggesting that, unlike the other invasive taxa, it may coexist with native vegetation and enhance forage availability. Riverine and ephemeral stream habitats had the highest invasive species densities (43.61 and 43.42 plants/m², respectively), while fence-line habitats had the lowest (0.96 plants/m²). Invasive species range and mean cover had a significant effect on invasiveness, including impacts on key elephant forage species ($F_{(2,8)} = 82.12$, $p < 0.01$, $R^2 = 0.94$). The most severe ecological impacts were observed in dry season foraging areas, particularly riparian and ephemeral stream-line habitats, where species diversity declined, leading to limited foraging opportunities for elephants. We recommend management actions through manual removal of high abundant and high impactful plant invasive species. Control efforts should prioritize species based on per capita effect and ecological impact ratings, with emphasis on riverine, stream-line, and roadside habitats.

Keywords: Invasive plant species, Ecological impacts, Food availability, Elephants, Habitat management

INTRODUCTION

Invasive species represent a significant and growing challenge to the integrity of protected areas globally, thereby undermining their core objective of conserving native biodiversity (Foxcroft *et al.*, 2017). Most invasive species are non-native, thus defined as organisms introduced outside their native geographic range, either intentionally or unintentionally through human action. Upon establishment, non-native invasive species often trigger profound ecological and economic impacts (Kumar & Singh, 2020; Shackleton *et al.*, 2015, 2019). On the other hand, native species as those indigenous to a locality or system.

Ecological disturbances, particularly soil disturbance, may facilitate the spread of non-native invasive species by altering resource and substrate availability, thereby offering windows of opportunity for establishment in the absence of competitors or predators (Dai *et al.*, 2025; Hobbs & Huenneke, 1992; Santoianni *et al.*, 2024). Disturbed ecosystems are therefore more vulnerable to invasion by non-native species (Foxcroft *et al.*, 2013). Moreover, conservation areas surrounded by human-modified landscapes face a high risk of invasive plant proliferation due to land uses that may provide propagules of invading species (Spear *et al.*, 2013; Ogunyebi *et al.*, 2018).

Many invasive species disrupt ecological processes and communities through habitat destruction, homogenization, and predation (King & Tschinke, 2008; Peh, 2010). For example, Shackleton *et al.* (2015) showed that *Prosopis juliflora* invasion reduced perennial grass cover from 15% where the *Prosopis* basal area was less than $2m^2$/ha to nil when the basal area was greater than 4.5 m^2/ha. Similarly, the cover of native perennial herbaceous plants declined from more than 20% to zero, as *Prosopis* cover increased.

Although few studies have examined the interactions between invasive species and megaherbivores particularly elephants in Kenya, Wells *et al.* (2022) demonstrated through exclosure experiments in the Laikipia rangelands of central Kenya that *Opuntia stricta* densities increased more rapidly in plots where large herbivores particularly elephants were excluded. Moreover, herbivore species diversity in general, and elephant density in particular, declined with increasing *Opuntia* density. Other less rigorous studies in Garissa (Huho & Omar, 2020) and Turkana county (Clement *et al.*, 2020) have also demonstrated that *Prosopis juliflora* reduces the availability of grazing resources for medium-sized grazing herbivores, such as Common Zebra, wildebeest, gazelles, and sheep, resulting from displacement of native forage grasses by woody thickets which limits access to palatable native species. Biological invasions have therefore been recognized as the leading driver of global biodiversity loss (Foxcroft *et al.*, 2017; Pyšek *et al.*, 2017; WWF, 2020).

Resource competition and availability limitation (Siddiqui *et al.*, 2021) can result in reduced food availability by out-competing or physically restricting access to native food plants (Oduor *et al.*, 2018), or modifying the behaviour of native animals (Stewart *et al.*, 2021). For example, the world's largest population of the great one-horned rhinoceros (*Rhinoceros unicornis*) has been shown to be imperilled by invasion of its principal food supply (grasslands) by *Mimosa rubicaulis*, *Mimosa diplotricha*, and *Mikania micrantha* in Kaziranga National Park, India, through impeded establishment of native palatable grasses (Lahkar *et al.*, 2011). Furthermore, invasive plants have been shown to transform woodlands and savannah ecosystems into grasslands through altered fire regimes, changed ecosystem processes, biodiversity loss, and pest outbreaks (Kenis *et al.*, 2009; Liebhold *et al.*, 2017; Peh, 2010). Given the propensity of invasive species to induce measurable changes in ecosystem properties, the ecological impacts of invasive species have become a key focus in the field of invasion ecology (Parker *et al.*, 1999; Pearson *et al.*, 2016; Ricciardi *et al.*, 2013).

In elephant habitats, the replacement of native forage species by invasive plants may lead to decreased native forage cover especially in dry savannas, where herbaceous forage is the primary food supply during the dry season (Das *et al.*, 2022; Schirmel *et al.*, 2016). Because invasive plants are well-defended against herbivory, this can influence the foraging behaviour of native herbivores by abstracting access to native food plants (Stewart *et al.*, 2021). Furthermore in key resource areas (Yoganand & Owen-Smith, 2014), such as riparian wetlands which serve as dry season grazing zones for herbivores preventing mass starvation (Illius & O'Connor, 2000), invasive species may have a higher influence on food biomass, especially during the dry seasons due to reduced species diversity and less available forage (Schirmel *et al.*, 2016).

Despite the progress made in understanding the impacts of non-native invasive species (Foxcroft *et al.*, 2017; Pysek *et al.*, 2012; Ricciardi *et al.*, 2013), quantifying their ecological impacts on herbivore food resources remains largely unexplored. This creates a major impediment in the management of plant invasions (Pearson *et al.*, 2016). In an attempt to fill that gap, this study investigated the distribution, invasiveness, and ecological impacts of non-native plants on native plants consumed by elephants and other herbivores in Mwea National Reserve.

In this study, the terms invasive or invasiveness were used to refer to the degree of success that non-native species attain within the introduced system. We hypothesised that an increase in the distribution, cover, and density of invasive plants reduced abundance and access to elephant food plants when compared to non-invaded areas. This can severely limit access to food resources for the African Elephant and other herbivores, leading to starvation and mortality. Given Mwea National Reserve's susceptibility to invasion due to ecological, geographical, and anthropogenic factors, and being an important refuge for a wide range of herbivore species, understanding the specific ecological impacts of non-native plants on elephant food resources is a critical step in the development of appropriate management protocols.

METHODS

Study area

The study was conducted in Mwea National Reserve, a 44Km^2 conservation area located at the confluence of rivers Thiba and Tana to form the Kaburu High Dam in Embu County-Kenya (Fig 1). The reserve is in a dry savanna ecosystem dominated by wooded grasslands, shrubland, and riparian woodland along the valleys of rivers Thiba and Tana, as well as the edges of Kaburu Dam. It's located at latitudes 0° 45' and 0° 52' South and longitudes 37° 35' and 37° 40' East and at average elevation of 950m-1150m above sea level. The climate of the reserve is predominantly semi-arid with annual rainfall range of 510mm to 760 mm. Rainfall distribution is bimodal with peaks in April and November. The mean minimum and maximum temperatures are 14°C and 30°C, respectively. The eastern and northern boundaries of the national reserve are fenced using a solar-powered electric fence to control human-wildlife conflicts with the surrounding farming communities. The dominant economic activity in the community surrounding the reserve is small-scale agriculture and horticulture, particularly along the riparian zones of the rivers Tana and Thiba. There are also several ephemeral streams that drain the nearby community land and flow across the reserve into Kaburu Dam, which is an important water reservoir for other hydropower dams downstream of the River Tana.

Plant Sampling Strategy

A purposive sampling strategy was used to select high-risk areas and sites already affected by Non-native invasive plant species in the reserve. This comprised areas around the fenceline boundary, along the reserve roads, riparian zones of the Thiba and Tana rivers, as well as along various ephemeral streams draining from the community settled areas. In total, 1,650 hectares of the study area were invaded by invasive species. Within the riparian areas of Thiba river, 408 hectares were invaded, the roadside and seasonal streams had each 385hectares of invasion while within the Tana river circuit 372 hectares were determined to be invaded. The fenceline was the least affected, with 100 hectares of invasion being measured. Standard 5m x5m sampling plots adapted from the global invader Impact network (Barney *et al.*, 2015), were placed randomly at the invaded site. The plots were suitable for invasive plants as they occurred in clumps of shrubs, forbs and tall herbs. The number of plots established at each site was proportional to the size of the invaded area.

To reduce spatial autocorrelation and edge effects bias, sampling plots were randomly set-out after every 50m and at least 10 meters from the linear sampling sites, such as fence-lines, usable roads, ephemeral streams or main river courses. A total of 85 random plots were set in different habitats and distributed as follows 5 plots along the fence-line, 20 on the roadside reserve, 20 on riparian land along the streams, 21 on the riparian zone of River Thiba and 19 in the riparian zone of River Tana.

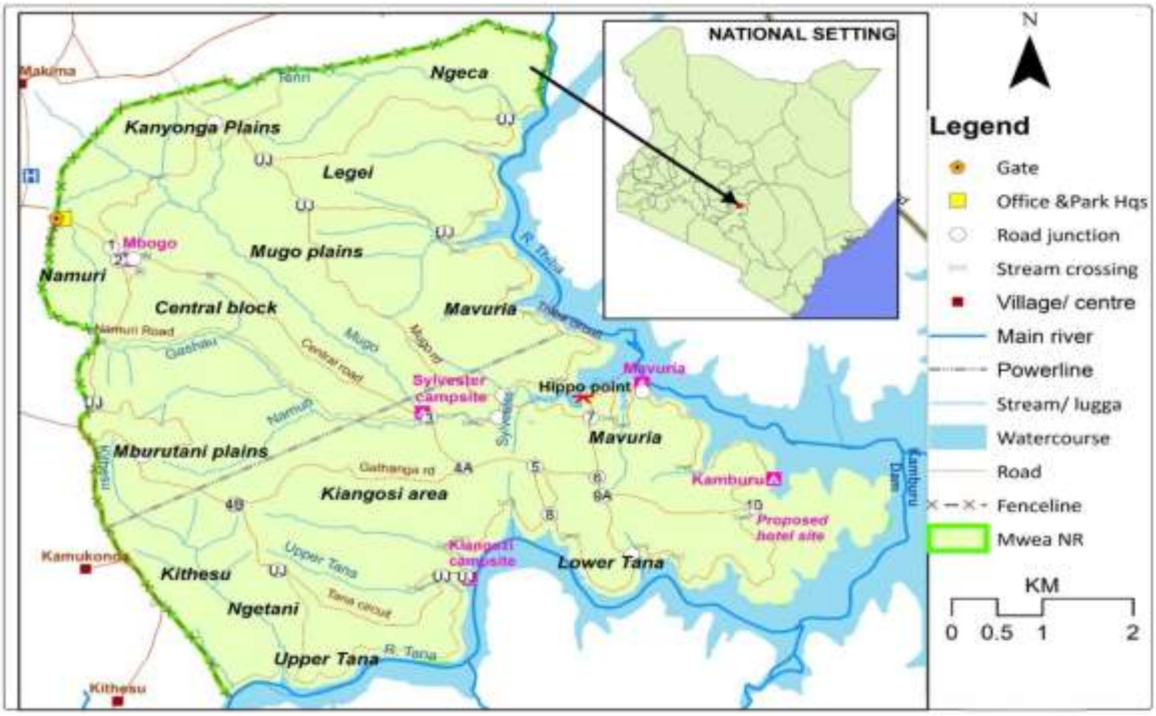

Figure 1: Map of Mwea National Reserve showing key habitat zones, Fence-line and riparian frontage

Sampling for invasive species was conducted during the dry season because of logistical mobility challenges, but the site monitoring was maintained across seasons. The position of each sampling plot was documented using a global positioning system (GPS).

Assessment of Invasive Plant Species Abundance, Diversity, and Distribution

The diversity of invasive plant species was sampled by targeting areas that met the following criteria:

i. Had the presence of invasive plants.
ii. Proximity to roads.
iii. Proximity to the fence-line (boundary).
iv. Along ephemeral streams.
v. Within riparian areas.

These areas had experienced some form of human disturbance or were considered essential pathways for the movement of invader propagules from the surrounding settlements into the protected area.

In the selected areas, we randomly established 5m x 5m sampling plots and documented the names and number of all plant species present, growth forms and categorized them into native or non-native invasive species. We also documented the habitat type at each sampling plot. Geographic attributes such as altitude, latitude, and longitude for each sampling plot were documented using a Global Positing System (GPS). Where the invasive plant species name was uncertain in the field, three samples were collected for identification at the University of Nairobi Herbarium. Thereafter, Vegan community ecology package in R statistical program was used to determine species diversity indices within the different sampled habitats. Diversity indices were used to compare the differences in invasion status within the different plant community types that were sampled for invasive species in the study area.

Factors Influencing the Distribution of Invasive Plant Species

Anthropogenic disturbances and ecosystem disruptions have been associated with the spread of invasive plants in many protected areas (Foxcroft *et al.*, 2017). In particular, flooding can promote the success of certain non-native invasive species by reducing biotic resistance and altering soil water conditions and nutrient availability (Thomaz, 2022). In this study we collected data on all disturbance types that could be attributed to the spread of invasive plants in each of the 85 random sampling plots within the study area, which included signs of anthropogenic driven disturbances, such as road earth-works, vegetation clearance, flooding, and fence-line construction. The probable dispersal pathways of invasive species propagules were also documented. Field observation data on human activities, including illegal entries for fuel-wood collection, charcoal burning, livestock grazing and honey harvesting were also documented. Observations and documentation of existing plant species were also carried out at the sites that regularly attracted high herbivore concentrations and recent road works so as to determine the focal points of the spread of invasive alien plant species in the study area.

Impacts of Invasive Plants on Key Food Resources for Elephants

To determine the ecological impacts and invasiveness of various non-native species in Mwea National Reserve, 5 m × 5 m random sampling plots were established in purposively selected vegetation types. Within each random sampling plot, all plant species present, including invasive species, were identified, and their percentage ground cover was visually estimated. The percentage cover of each species was used as a measure of its abundance at each sampling site. In total, the percentage cover for all plant species (both invasive and native) was estimated across 85 sampling plots. For each plot, the combined percentage cover of all species was standardized to equal 100%. Additionally, the geographic coordinates of each sampling plot were recorded using a global positioning system (GPS). These waypoints were later downloaded and merged with species occurrence data in an ArcGIS environment. The percentage cover of different species was used as a measure of their abundance. For each sampling plot, geographic coordinates were recorded using a Global Positioning System (GPS) device. The coordinates were later downloaded and merged with the corresponding species abundance data for each plot.Invasiveness of the different invader species were quantified using the following formulae: Invasiveness = Species range(in square meter X Abundance (percentage coverage) (Parker *et al.*, 1999; Pearson *et al.*, 2016).

The ecological impacts of each non-native invader species on native species was determined by fitting a linear mixed-effects model with the percentage cover of native species as the response variable using the formulae developed by Pearson *et al.*, (2016) as follows: Total ecological Impact (I) = R x A x E where *I* is the total impact of each invasive species, *R* is the range in m^2 multiplied by the area of each sampling plot (i.e. 5m x5m), *A* is abundance denoted by the total percentage coverage of each species in the different sampling plots and *E* is the per capita effect which represented the effect per unit cover of each invasive species on native vegetation (Parker *et al.*, 1999; Pearson *et al.*, 2016), was determined using linear mixed-effects models in the R statistical environment (R Core Team, 2024). The percentage cover of native species was used as the response variable. Each focal invasive species was included separately as a fixed effect predictor, while the combined cover of all other invasive species was entered as a single aggregated covariate. Habitat type (riverine, roadside, fence line, streamline) was treated as a random intercept to account for non-independence of sampling plots within habitats.

The slope coefficient (β) of the focal invader in each model was interpreted as its per capita effect on native plant cover. We fitted eleven models using the lme4 package in R**,** one for each invasive plant species, while holding the effect of the remaining invaders constant. Other invasive species were not analysed individually but were considered collectively to influence the availability of elephant food plants. The model assumptions were evaluated by examining residual plots for homoscedasticity and normality. The dependent variable was calculated as the total percentage cover of all native plant species recorded per plot. The synergistic effects among invaders in influencing per capita effects were accounted for by including the interaction effects of focal invader cover, other invaders cover and habitat type occupied by the invader species.

RESULTS

Impacts of Invasive Plants on Species Diversity in Mwea National Reserve

This study was meant to address the question as to whether non-native invasive species reduced availability of elephant food plants in Mwea National Reserve. Findings indicated that in different sampled habitats, there is high potential for invasion of the MNR by invasive plant species particularly within the riparian areas because of its downstream location and community managed surrounding agricultural landscape. Most of the invasive species were short shrubs and tall herbs. These plants mainly affect elephant food plants by hindering plant growth and regeneration as well as changing vegetation structure, which has profound adverse effects on herbivore community structure and survival, especially in small conservation areas.

Due to differences in levels of invasion within the different sampled habitats, there was differences in species diversity. The fence-line habitats exhibited the highest diversity, with a Shannon–Weiner index (H) of 2.28 and a Simpson's index (D) of 0.84. In contrast, riverine habitats had the lowest species diversity (H = 0.51; D = 0.15) and evenness (J = 0.11). Roadside and ephemeral streamline habitats were characterized by intermediate species diversity (H = 0.76; D = 0.23) and (H=0.62; D=0.18) respectively. However, species evenness in these areas were low (J = 0.18 and 0.14). The low species diversity and evenness within the ephemeral streams was due to increased levels of invasion by *Parthenium hysterophorus*, *Senna didymobotrya*, *Senna longiracemosa* and *Xanthium strumanium*

Overall, fence-line habitats supported the most balanced plant communities while the riverine areas were dominated by invasive species resulting in reduced diversity and evenness

Table 1: Species diversity indices within different habitats sampled for invasive species in Mwea National Reserve

Habitat type	Shannon-Weiner (H)	Simpson D)	Evenness (J)	Margalef
Fence line	2.28	0.84	0.68	4.38
Roadside	0.76	0.23	0.18	6.85
Stream side	0.62	0.18	0.14	6.16
Riverine	0.51	0.15	0.11	8.27

Diversity and Distribution of Invasive Plant Species in Mwea National Reserve

A total of eleven invasive plant species belonging to five families were recorded in Mwea National Reserve. *Parthenium hysterophorus* was the most dominant species, representing 98.6% of all sampled individuals. The dominance of *P. hysterophorus* indicates a strong invasive potential, likely driven by its high reproductive capacity allelopathic properties, and ability to colonize disturbed habitats, particularly along riparian zones. In contrast, the other ten invasive species occurred at much lower frequencies and together accounted for only 1.4% of the total recorded individuals (Table 2)

Table 2: Invasive plant species occurrence frequency in Mwea National Reserve

Species Name	Frequency of occurrence
Parthenium hysterophorus L.	76233
Senna longiracemosa (Vatke) Lock	650
Xanthium strumarium F.	556
Megathyrsus maximus (Jacq.) B.K.Simon & S.W.L.Jacobs	167
Senna didymobotrya (Fresen.) H.S. Irwin & Barneby	112
Senna occidentalis L.	44
Senna spectabilis (DC.) H.S.Irwin & Barneby	22
Lantana camara	18
Leucaena leucocephala(Lam.) de Wit	12
Datura stramonium L	7
Datura metel	2

Habitats associated with water, particularly along riverine and seasonal streams, had a high density of invasive species, resulting from increased disturbance incidents and nutrient-rich soils from community areas. On the other hand**,** the low density of invasive species within the fence-line habitats suggests that these areas currently present minimal invasion risk. Roadsides supported a moderate density of invasive plants, likely due to disturbances from vehicle movement and soil exposure (Figure 2). Generally, shrub-dominated areas displayed the highest degree of invasion by alien species, suggesting that structural characteristics of these habitats, such as low canopy cover, high disturbance from browsing herbivores and soils conditions may have provided favourable niches for non-native invasive plant species establishment and growth. In contrast, grass dominated dense ground cover provided by native grass acted as a biological resistance barrier**,** reducing opportunities for invasive plants colonization within the grassland habitats. Unlike other invasive plants, *M. maximus* was utilized by elephants as forage but in few isolated instances and especially during the dry season when other forage species were not available.

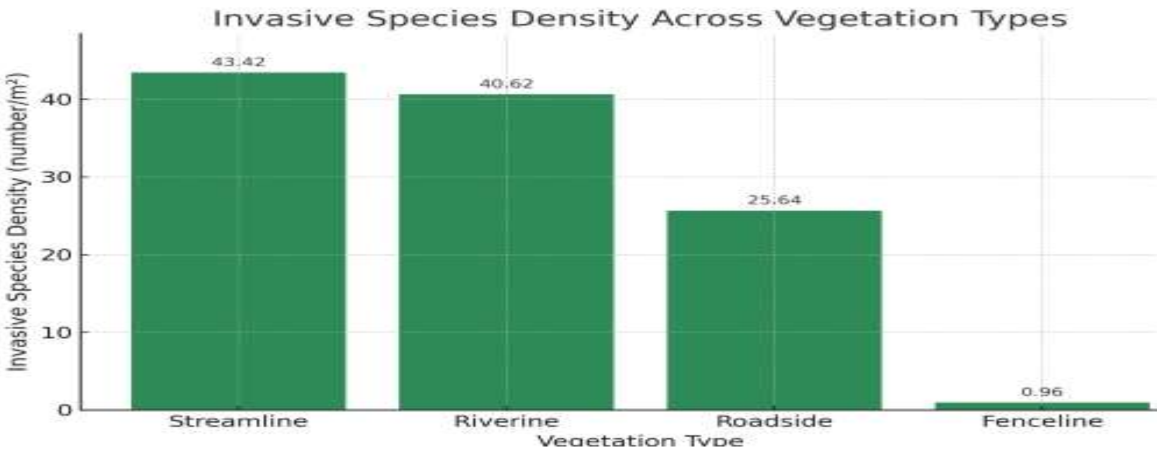

Figure 2: Invasive species density across vegetation types in Mwea National Reserve

There were no significant differences in the mean abundance of invasive species among the four habitat categories sampled ($F_{(3,40)}$ = 0.51, p = 0.67, ω^2 = 0). Levene's test for homogeneity of variances was not significant ($F_{(3,40)}$ = 0.08, p = 0.67), confirming that the assumption of homogeneity of variances was met and therefore, the use of ANOVA was appropriate.

Factors that Influence the Distribution of Invasive Plant Species in Mwea National Reserve

Ecological and anthropogenic-related disturbances were found to influence the spread and proliferation of non-native invasive species in Mwea National Reserve. Regular flood-related disturbances, including transportation and deposition of silt in the river or stream valleys, were attributed to the high densities of invasive plant species. Seasonal water run-offs from the settled community land through ephemeral streams were ranked second in facilitating dispersal of invasive plant species propagules, while road construction and maintenance, as well as vehicular traffic, were ranked third. The disturbance category with the least influence on invasions in the study area was associated with fence clearance and human-induced edge effects, as shown in Figure 3.

Log-transformed invasive species densities did not differ significantly among the habitats sampled ($F_{(3, 20)}$ = 1.33, p = 0.293). Levene's test confirmed the assumption of variance homogeneity W = 0.28, p = 0.839). Nevertheless, effect size estimates indicated ecologically meaningful differences with eta squared (η^2 = 0.166), implying that 16.6% of the variance in densities was attributable to habitat.

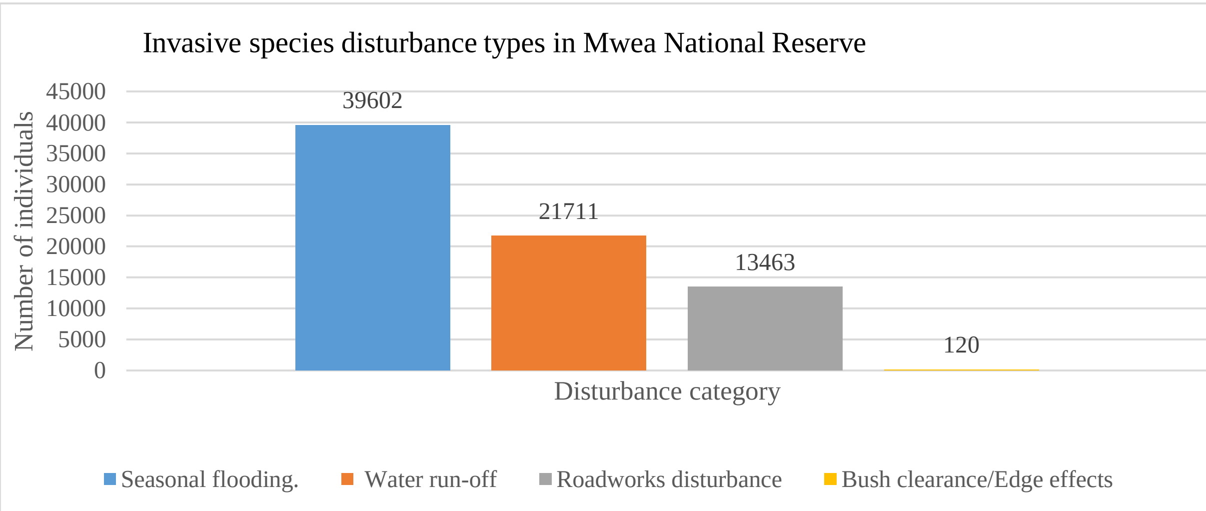

Figure 3: Frequency of invasive species within different disturbance categories in Mwea National Reserve

Invasive Species Dispersal Vectors

Water was the most important transport vector for invasive species in Mwea National Reserve. Most invasion records were either associated with ephemeral streams or perennial rivers. Similarly, invasive plants inhabited topographic depressions where water from rainfall and silt –ladden run-off settled during the wet periods. Vehicular traffic was the second important contributor to invasive plant species dispersal as invasions appeared to originate from the road sides. Birds, ants, termites and rodents may also have played a role of dispersing propagules of invasive plant species but on a localized scale. Therefore, water flow in the seasonal streams from community lands through the reserve and the two permanent rivers were the main dispersal agents contributing to the proliferation of invasive plant species in Mwea National Reserve.

Invasiveness of Different Non-Native Invasive Plant Species

The prolific seed producing herb *Parthenuim hysterophorus* was the most invasive non-native species in Mwea National Reserve. This noxious weed is rapidly spreading from road sides, riparian areas and ephemeral streams. Other notorious plant invaders were *Senna didymobotrya, Xanthium strumanium, Senna longiracemosa* and *Megathyrsus maximus.* These invaders were mostly found within the riparian areas along rivers Tana, Thiba and kaburu dam as well as along the valleys of ephemeral streams underscoring the vulnerability of dry season grazing riparian areas to invasion by non-native invasive species. The least invasive plant invasive species *Leucaena leucocephala*, which was sparsely scattered with discernible distribution pattern in the reserve (Table 3).

Table 3: Non-native species percentage invasiveness in Mwea National Reserve

Species Name	Total % cover	Range in M^2	Mean % cover/M^2	% Invasiveness
Parthenium hysterophorus	3819.5	1925	1.984	3819.4
Senna didymobotrya	261.2	475	0.55	261.2
Xanthium strumarium F.	92.3	400	0.231	92.3
Senna longiracemosa	73.5	250	0.294	73.5
Megathyrsus maximus	71	875	0.081	71
Senna occidentalis L.	17.3	150	0.115	17.3
Senna spectabilis	11.7	175	0.067	11.7
Lantana camara	8.7	125	0.07	8.7
Datura stramonium L	0.2	50	0.004	0.2
Datura metel	0.2	25	0.008	0.2
Leucaena leucocephala	0.2	50	0.004	0.2

Notes: Non-Native species invasiveness calculated as the product of species range in meter squared and mean percentage cover per meter square (R X A) (Parker *et al.*, 1999)

Invasive species range and mean cover explained 94% of the observed variance of invasiveness $F(2,8) = 82.12.\mathrm{P} < 0.01,\ R^2 = 0.94$). Mean invasive species percentage cover had significant effect on invasiveness (P<0.01). Within the different habitats sampled, *Parthenium hysterophorus* was the most invasive non-native species with invasiveness being highest within the riverine habitats followed by the ephemeral stream edge habitats, road side and least being within the fence-line habitats mainly due to increased propagule loads and high disturbance levels.

Ecological Impacts of the Different Invasive Plant Species in Mwea National Reserve

Ecological impacts on native plants diversity (percent reduction in native cover) were mostly contributed by *Parthenium hysterophorus, Senna didymobotrya, Xanthium strumanium* and *Senna longiracemosa* due to their strong negative per capita effects (β) on native species cover. The least impactful was *Leucaena leucocephala* (Table 4). Interestingly, *Megathyrsus maximus,* though non-native exhibited a positive association with native cover (β = +0.22), suggesting that its presence didn't suppress the growth of native vegetation and

Table 4: Ecological impacts of invasive plant species in Mwea National Reserve, Kenya

Invasive species name	Range in m²	Mean % cover	Per capita effect (β)	% Impact
Parthenium hysterophorus L.	1925	1.98	-0.82	-3125.43
Senna didymobotrya	475	0.54	-0.38	-97.47
lantana camara	125	0.07	-0.65	-5.6875
Xanthium strumarium F.	400	0.23	-0.27	-24.84
Senna longiracemosa	250	0.29	-0.29	-21.025
Datura stramonium L.	50	0.004	-0.05	-0.01
Megathyrsus maximus	875	0.08	+0.22	15.4
Senna occidentalis L.	150	0.12	-0.55	-9.9
Datura metel	25	0.01	-0.12	-0.03
Senna spectabilis	175	0.07	-0.40	-4.9
Leucaena leucocephala	50	0.00	-0.44	0

The impact scores are calculated as the product of species range (m²), mean percentage cover per plot, and per capita effect on native species abundance. Per capita effects were derived from slope parameters (β) *in a mixed-effects regression of native species cover against focal invader cover while controlling for the effect of other invaders and habitat as random effects*

was utilized as forage by elephants within the study area during the dry season. Species range, mean abundance, and *per capita* effect explained 95.7% of the variance in invasive species impact (R^2 = 0.957). There was a significant relationship between the three predictor variables and impact ($F_{(3,7)}$ = 75.974, p<0.01). However, the mean invasive species percentage cover had the largest influence on the overall impact of all the invasive species in the study area (t = 5.58, P<0.01). Range, on the other hand, had the least effect on invasive impact (t = 0.836, p = 0.43).

DISCUSSIONS

This study explored the diversity and distribution of invasive plant species in Mwea National Reserve. We determined invasiveness and ecological impacts of non-native invasive plant species on key resources for herbivores including the elephants using quantitative methods. Eleven non-native invasive species from five families were identified in the study area comprising of the following species, *Parthenium hysterophorus L, Senna didymobotrya, Lantana camara* L., *Xanthium strumarium* L, *Senna longiracemosa, Datura stramonium, Megathyrsus maximus, Senna occidentalis, Datura metel, Senna spectabilis, and Leucaena leucocephala.* Among the invasive plant species documented in Mwea National Reserve, *Parthenium hysterophorus L.* was the most widespread likely due to its high seed production, dual C3/C4 photosynthetic cycles, early maturity, tolerance to diverse climatic and disturbance levels, allelopathic potential, and un-palatability to herbivores (Tiawoun *et al.*, 2024). This could have enabled it to outcompete native species especially within riparian habitats that acted as dry season grazing areas for elephants and other herbivores.

The dominance of *Parthenium hysterophorus* and high per capita effect suggest a strong negative impact on native biodiversity, making it a priority for management interventions. In contrast, the low range and high per capita effect exhibited by *Lantana camara* underscores the need for prioritized management interventions due to its high potential to establish dominance, competitive advantage, and high ecological impacts that may exclude native plant species, thereby compromising forage availability for elephants. Other ecologically high impactful invasive species, including *Senna didymobotrya*, *Xanthium strumarium*, and *Senna longiracemosa*, were not utilized by resident herbivores as food and exhibited high germination rates and fecundity. These specific traits have been shown to increase invasion success(Ens *et al.*, 2015; Gioria & Pyšek, 2017; Moravcová *et al.*, 2010; Van Kleunen *et al.*, 2010), and ecological impacts (Ahsan *et al.*, 2016). The synergistic effects of the above attributes and environmental disturbances that alter the physical environment (Turner, 2010), are probable causes for high non-native plant species invasion of Mwea National Reserve.

Ecological disturbances and species traits have been identified as key factors influencing the establishment and spread of invasive species (Catford *et al.*, 2012; Orbán *et al.*, 2021). In particular, flooding disturbances are known to enhance the success of certain non-native invasive species by reducing biotic resistance or altering resource availability in riparian areas(Perry *et al.*, 2018; Thomaz, 2022). Findings from our study support this observation, as water flooding and surface runoff in ephemeral streams played a significant role in the dispersal and establishment of invasive species propagules. Consequently, surface runoff from nearby community settlements, along with land-use changes and climate variability, may have contributed to the introduction and spread of invasive species into the reserve, leading to increased invasions and the homogenization of some habitats through dominance by non-native invasive species.

Dispersal pathways such as water flow and road networks contributed most to the spread of non-native invasive species in Mwea national Reserve resulting to high density in riverine and ephemeral streams habitats, likely resulting from frequent and regular recharge of invasive species propagules. These results support findings by Thiele *et al.*, (2008) that roads and river corridors significantly increase invasion risk of many ecosystems.

Although no significant differences in the densities of invasive species were detected across various habitats, the effect size ($\eta^2 = 0.166$) indicates that habitat could have an ecologically significant influence on the distribution and density of these species. Since 16.6% of the variance in invasive species densities can be attributed to habitat differences, it is probable that habitat-related differences in invasive plant densities exist. Furthermore, the occurrence of high invasive species density and diversity along the river channels and roads can be explained by regular soil disturbance resulting from seasonal flooding and run-off which introduces diverse substrates and create new ecological niches for invasive species. Road construction and vehicle use could have a facilitative role as Compaction by vehicles reduces native plant vigour creating areas with limited native species competition. Moreover, changes in soil structure during road construction (Son *et al.*, 2024), have been shown to drive land-cover change, making natural ecosystems susceptible to invasion (Gelbard & Belnap, 2003). Additionally, vehicle movement and roadwork operations can introduce non-native invasive plant seeds into un-infested areas, while maintenance activities may create favourable conditions for seed germination and establishment (Gelbard & Belnap, 2003; Vakhlamova *et al.*, 2016).

Edge effects had limited influence on invasive species dispersal, implying that most propagules originated from the broader catchment and were transported into the reserve by water or vehicular traffic associated with road construction and maintenance. These results contradict the view that edge effects play a key role in biological invasions (González-Moreno *et al.*, 2013; Ohlemüller *et al.*, 2006). Instead, dispersal vectors related to water flooding, runoff, and road-works were the most important factors influencing invasive species establishment. The high influence of water may have been exacerbated by fertilizer use in the surrounding farms, leading to increased nutrient availability and healthy seeds while regular flooding and run-off may likely have increased propagule pressure, facilitating non-native establishment. Hydrochory has been cited as the main pathway for the delivery and dispersal of invasive species in riparian habitat (Jones *et al.*, 2020; Mao *et al.*, 2019; West *et al.*, 2020).

Consistent with previous research (Bekele *et al.*, 2019; Kenis *et al.*, 2009; Shackleton *et al.*, 2015) the study found that increased invasive species diversity and density reduced overall species diversity. High species diversity and evenness along the fence-line compared to other sampled habitats indicate that edge effects had a low influence on alien species introduction. In contrast, riverine and ephemeral stream habitats exhibited low diversity indices due to high dominance by invasive species. High abundance of invasive plants reduced species diversity and evenness through competitive exclusion and dominance leading to low foraging opportunities available to herbivores. These results align with findings by Catford *et al.* (2012); Schirmel *et al.* (2016) which showed that increased invasive abundance significantly impacts species evenness and diversity (Bradley *et al.*, 2019).

Although several species traits contribute to invasiveness (Catford *et al.*, 2012; Catford & Jansson, 2014), species range and mean percentage cover were the most important indicators of invasiveness. *Parthenium hysterophorus*, *Senna didymobotrya*, *Xanthium strumarium* and *Senna longiracemosa* were highly invasive due to their extensive spread and high mean percentage cover. Similar results by Pearson *et al.* (2016), showed that non-native species' range and local abundance influence both invasiveness and ecological impact due to changes in ecosystem properties, particularly through the displacement of native species by non-native invasive plant species (Pyšek *et al.*, 2012; Ricciardi *et al.*, 2013). Furthermore, these impacts depended on invasive species abundance and per capita effects (Parker *et al.*, 1999; Pearson *et al.*, 2016; Ricciardi *et al.*, 2013; Yokomizo *et al.*, 2009).

Based on the available data, there's an indication that seasonal differences in invasive species ecological impact exist within the study area. Negative impacts were most pronounced during the dry season, when elephant and other herbivore densities increased within the dry season foraging areas, and most annual plant species many of which serve as elephant forage had senesced after seed dispersal. In contrast, during the wet season, the regeneration of annual plants and shrubs alleviated competitive pressures, thereby reducing the ecological impact of invasive species. However, further research that incorporates a comparison of multiple dry and wet seasons to ascertain the indicative finding of this research is recommended. Since dry-season forage availability is a critical determinant of herbivore population size and survival (Illius & O'Connor, 2000; Yoganand & Owen-Smith, 2014), the invasion of riparian areas by alien plants threatens wildlife sustainability in Mwea National Reserve by reducing the availability of key food resources for large-bodied herbivores such as elephants and buffalo (Fynn *et al.*, 2015; Yoganand & Owen-Smith, 2014).

Elephants in the study area foraged on a variety of tall perennial grass species, shrubs, short trees, as well as branches, bark, and roots of tall trees such as *Senegalia ataxacantha*, *Polygala tourn*, *Clausena anisata*, and *Cyperus papyrus*. These results support earlier finding by Chira (2005). Where elephants were demonstrated to show strong preference for several native species such as *Senegalia mellifera*, *Commiphora africana*, *Combretum aculeatum*, *Grewia tembensis*, and *Grewia bicolor* in the same study area. The proliferation of non-native plant species may have negatively affected the regeneration and growth of key forage species potentially altering vegetation structure and limiting food resources availability for elephants. Strong negative effects were exerted by species with high per capita impacts particularly *Parthenium hysterophorus Senna didymobotrya*, *Xanthium strumarium*, *Senna longiracemosa* and *Lantana camara*. In line with competitive exclusion principle, these invaders likely suppressed native plant communities through resource competition and allelopathic interference resulting to reduced availability of key forage resources for elephants. Contrastically, positive association of *Megathyrsus maximus* with native cover, suggests a potential for case enhanced elephant forage availability, and may provide novel foraging opportunities during the dry season and prolonged droughts. Such resource dynamics may buffer against seasonal forage scarcity, increase dietary diversity, and support habitat use in areas where native forage species are limited. These findings therefore underscore the importance of prioritising management interventions against invasive species with high per capita effects and invasiveness as their uncontrolled proliferation threatens ecosystem resilience compromising the long-term availability of critical forage resources for herbivore populations within the reserve.

CONCLUSION AND RECOMMENDATIONS

Invasive plant species present a serious challenge to the management of conservation areas. Protected area managers must therefore not only prevent further incursions and establishment of invasive plants from surrounding agricultural landscapes but also control the spread of non-native invasive already established within their reserves. Since no single isolated approach is likely to be effective, we recommend the adoption of integrated management strategies that combine multiple control methods. Herbicides are highly discouraged as they have the potential of poisoning essential water resource. On the other hand, biological control methods may not be feasible as no browsers have been shown to utilise majority of the invasive plants in the study area.

To enhance efficiency and reduce operational costs, management efforts should prioritize high-risk zones and already affected areas, especially those with high levels of disturbance, such as roadsides and riparian habitats. A landscape-level approach is essential, involving collaboration with multiple stakeholders, including local farming communities, to raise awareness, strengthen monitoring, and control of invasive species in surrounding agricultural lands, which often serve as the primary sources of propagule pressure. Within the reserve, managers should also actively monitor vegetation dynamics and the movement of large herbivores, which may increasingly act as dispersal agents of invasive propagules. Given that invasiveness and per capita effects strongly determine ecological impact, priority management actions in Mwea National Reserve should focus on reducing the abundance, cover, and impacts of the most problematic species: *Parthenium hysterophorus*, *Senna didymobotrya*, *Xanthium strumarium*, *Senna longiracemosa*, and *Lantana camara*. Targeted interventions in sensitive areas such as riverine zones and road verges are particularly critical to limit further spread and ecological disruption.

Conflict of Interest

We declare no conflict of interest in undertaking this work.

Data Availability Statement

The data that support the findings of this study are available from the University of Nairobi Repository https://erepository.uonbi.ac.ke/ or from the corresponding author.

Ethics Approval Statement

This study was approved by the National Commission for Science, Technology and Innovation (NACOSTI)-Kenya under license number 629485.

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