

Impacts of invasive alien species on riparian plant communities in South African savanna

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Research Article

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Abstract

Biological invasions are a threat to protected areas globally; however, the relative lack of studies quantifying the ecological impacts impairs informed decision-making. We selected three annual alien plants, widespread in the riparian habitats of the Kruger National Park, South Africa: *Datura innoxia*, *Parthenium hysterophorus*, and *Xanthium strumarium*, to examine their potential impacts on riparian plant communities. We identified 12–13 populations for each and placed a pair of invaded and uninvaded plots in each population. Species richness, Shannon diversity, and Pielou evenness were compared between the invaded and uninvaded plots using LMM models, and species composition was compared using ordination. The invaded vegetation showed lower species richness compared to the uninvaded, with the strongest effect observed for *P. hysterophorus*. The invaded plots also showed lower Shannon diversity and Pielou evenness due to the presence of alien dominants. For all three invaders, the invasion resulted in changes in the composition of native vegetation. Some native plants were more frequent and abundant in the invaded vegetation, possibly due to the habitats created in sandy river beds. The native species richness decreased with increasing invader cover, but the species richness of aliens accompanying the invasive dominants was not negatively affected by their cover. Our results confirmed the negative impact of invasive aliens on native plant diversity, with the most pronounced effect by *Parthenium hysterophorus* invasions.

Introduction

Globalization has led to a significant rise in the rate at which species are being introduced to regions beyond their natural areas (Roy *et al.* 2023, Seebens *et al.* 2021). While only a small proportion of introduced species become invasive (i.e., survive and spread over long distances in the introduced areas, Richardson *et al.* 2000), invasive species can have dramatic environmental and socioeconomic impacts (Bacher *et al.* 2018, Kumschick *et al.* 2020), and biological invasions are among the major threats to biodiversity globally (Brondizio *et al.* 2019, Roy *et al.* 2023). In the last decade, knowledge of the global distribution of alien organisms has increased dramatically (Pyšek *et al.* 2020b), as has awareness of invasions in protected areas (Foxcroft *et al.* 2017, Shackleton *et al.* 2020). While protected areas are frequently the focus of intensive ecological research programmes, the effect of biological invasions is comparatively poorly studied (Hulme *et al.* 2014), leading to a lack of quantitative data on impacts on which to base decisions.

Protected areas were shown to act as barriers to invasions by alien plants (Foxcroft *et al.* 2011, Pyšek *et al.* 2003) and offer refuge from invasive species under climate change (Gallardo *et al.* 2017). However, alien species still penetrate into protected areas, and nowadays, very few are known to be free of invasive species (Pyšek *et al.* 2017, 2020b). In addition, the number and magnitude of alien plant invasions in protected areas are increasing; this trend is most pronounced for invasive plants that pose the greatest continued threat of all taxonomic groups, as their numbers in protected areas worldwide have increased by ~30% compared to the situation 40 years ago (Shackleton *et al.* 2020). Impacts by alien species have been shown to be as significant inside protected areas as outside, but only a small proportion provide actionable management recommendations (Hulme *et al.* 2014). Invasive plants are being introduced into protected areas by various means associated with human activities (ornamental species, tourism, vehicles), but also naturally via water courses (Foxcroft *et al.* 2011, Foxcroft *et al.* 2019, Jarošík *et al.* 2011). Thus, efforts to protect these areas from plant invasions are constrained by the introduction of alien species' propagules. For example, rivers entering protected areas represent a big risk, as one cannot control what they bring in. Studies showed that the number of alien invasive

plants inside a protected area could be predicted by several factors, of which water runoff from adjacent areas was the most important one (Foxcroft *et al.* 2011, Jarošík *et al.* 2011).

Rivers have long been recognized as major pathways of alien plant introductions. On the one hand, most rivers flow through human settlements, from which they can carry propagules of alien plants into riparian sites (Hood & Naiman 2000, Planty-Tabacchi *et al.* 1996). Moreover, fluctuating water levels in riparian areas may facilitate the establishment of these propagules since they provide open spaces by removing existing vegetation and increase available resources by depositing nutrients (Richardson *et al.* 2007). As a result, alien plants often concentrate in riparian sites (e.g., Chytrý *et al.* 2008, Pyšek *et al.* 2010), and while some remain restricted to the vicinity of the river, often after a considerable time lag, some spread away from the river (Čuda *et al.* 2020, Pyšek *et al.* 2020b). This represents a major threat to vegetation beyond the riparian ecosystems and can start new invasions into habitats previously unaffected.

Our knowledge of the dynamics and mechanisms of riverine invasions is largely based on temperate climatic regions (Planty-Tabacchi *et al.* 1996, Pyšek *et al.* 2010). However, the role of rivers in invasions in subtropical and tropical regions may differ from those in temperate regions, where water levels are permanently high and invading plants spread along rivers by colonizing their banks. In subtropical arid regions, where water levels fluctuate depending on the season, invasive populations may occur directly in riverbeds which makes their invasion dynamics more closely dependent on channel dynamics and stream features (Sibiya 2019) long-term weather patterns, and water level fluctuations (Foxcroft *et al.* 2007, Richardson *et al.* 2007, Sibiya 2019). The macro-channel floor in perennial river in ecosystems such as African savannas is formed by a mosaic of water and terrestrial patches, with the balance between the two environments dynamically changing, thus providing a permanent opportunity for the establishment of arriving invaders (Foxcroft *et al.* 2008, Sibiya 2019). Arid ecosystems are, in global comparison to other biomes, less invaded; this is due to several factors, such as the limited introduction of alien plants to these areas or the ability of native plants to resist stressful conditions (Pyšek *et al.* 2017). However, invasions in these areas can have devastating consequences (see Milton & Dean 2010 for review).

Much work has been done on the impacts of invasive alien trees and woody shrubs on river ecosystems (e.g., Beater *et al.* 2008, Esler *et al.* 2008, Witkowski & Garner 2008), with some work on the management of annual and perennial shrubs and herbaceous species (Morris *et al.* 2008). Unfortunately, to our knowledge, the fine-scale spatial dynamics in relation to invasions and their impacts on native plant communities has been little studied in subtropical and tropical riparian habitats (see Foxcroft *et al.* 2008 and Sibiya 2019 on patterns of alien plants across river geomorphology). To predict future invasions and provide managers and policymakers with a scientifically sound basis to support decision-making, understanding the impacts associated with pathways of invasion, such as rivers, is a key element (Hulme *et al.* 2008).

Therefore, in this study, using Kruger National Park (KNP) as a model subtropical/tropical African savanna ecosystem, we focus on analysing the impact of three major herbaceous invasive species spreading along rivers on riparian savanna vegetation. The study is a contribution to the broader MOSAIK (Monitoring Savanna Biodiversity in Kruger National Park) project that explores patterns of species diversity across habitats

in KNP (Delabye *et al.* 2022, Hejda *et al.* 2022, Pyšek *et al.* 2020a, Pyšková *et al.* 2022b). Specifically, we asked (i) what are the impacts of plant invaders generally, and by each dominant invasive species, on the plant community characteristics such as species richness, diversity, and evenness; and (ii) do invasions result in changes in plant species composition, also with regards to the native and alien status of the associated species?

Material and methods

Study area: Kruger National Park

Kruger National Park, established in 1898 and formally proclaimed in 1926, is the largest national park in South Africa and one of the oldest national parks in the world. It is located in the north-eastern part of the country, covering an area of 19,169 km² and stretching ~450 km north-south and 84 km east-west. The majority of KNP has a subtropical climate, with the Tropic of Capricorn crossing the park in the North, and several large rivers flow through the park, mostly in a west-east direction (i.e., Sabie, Olifants, Crocodile, Letaba, Shingwedzi, Luvuvhu and Limpopo). The park's environmental heterogeneity stems from diverse geological conditions (granitoid bedrock in the western vs. volcanic, mainly basalt and gabbro, in the eastern part), altitude (140–780 m a.s.l.), climate (450–750 mm of annual precipitation), and vegetation (Hejda *et al.* 2022, MacFadyen *et al.* 2016). According to the latest update (Foxcroft *et al.* 2023), there are an estimated 146 alien plant species occurring in the wild in KNP, of which 30 are casuals, 58 are naturalized, 21 have become invasive, and for 37 species, the status remains to be determined (status categories according to Richardson *et al.* 2000). In response to the escalating importance of plant invasions, KNP has initiated several programmes aimed at preventing and mitigating incursions of alien species (Foxcroft & Freitag-Ronaldson 2007, Foxcroft *et al.* 2009, Koenig 2009), but to date, few studies investigated the impact of major invaders on plant community characteristics (Foxcroft *et al.* 2008, Novoa *et al.* 2021, Robertson *et al.* 2011).

Study species

We focused on three major invasive species in KNP (Figure 1), whose selection was based on the following criteria: (i) they occur in riverbeds, where they dominate the invaded communities and form extensive stands (so that they are likely to have impacts on the river channel and adjacent riparian ecosystem); and (ii) they are controversial species of concern to KNP management because little is known about their impacts, potentially leading to the assumption that they are minor (especially for *Xanthium strumarium* and *Datura* spp.), and therefore, management recommendations are urgently needed. They represent a potential threat to savanna vegetation as they have successfully naturalized or become invasive, both globally and in other African countries (Table 1). *Datura innoxia*, *Parthenium hysterophorus*, and *Xanthium strumarium* are the species that best meet these criteria and represent the most problematic annual plant invaders in KNP. *Parthenium hysterophorus* largely occurs in the southern region of KNP, while *D. innoxia* and *X. strumarium* are typically found in high abundances in the northern region of the KNP (Figure 2).

Sampling design and data

The plots invaded by the target species were sampled along Sabie, Letaba, Olifants, and Shingwedzi rivers (Figure 2). We located 12–13 populations of each invader in river beds and/or on river



Figure 1. Invasive alien species studied (a, c – *Datura innoxia*, e – *Parthenium hysterophorus*, g – *Xanthium strumarium*) and various types of uninvaded control plots (b, d, f) adjacent to those dominated by the invaders. Photos by P. Pyšek.

banks, distributed across 5, 6, and 7 sites per species (for *D. innoxia*, *X. strumarium* and *P. hysterophorus*, respectively). Within each population, we established a plot of 100 m² with the invasive species dominating the vegetation, reaching at least 50% cover. The majority of plots were 10 × 10 m; where the character of the population did not allow to place a square, a different shape was used to achieve the same total cover (e.g., 8.0 × 12.5). For each invasive population, we located a plot of the same size in the adjacent uninvaded vegetation located in similar habitat conditions, representing the control (see Hejda *et al.* 2009 for details and potential caveats of the space-for-time substitution approach). This design resulted in 74 plots (37 invaded and 37 uninvaded, arranged in pairs) spread over 18 sites by four rivers (Figure 2), where the vegetation was sampled.

All plant species present in the herb layer of a plot were recorded, and their abundance was estimated using the Braun-Blanquet cover-abundance seven-grade scale (Mueller-Dombois & Ellenberg 1974); shrubs of height comparable to the surrounding herbs were included in the herb layer. This yielded the data on species richness, represented by the total number of species recorded in a plot. To quantify the occurrence of species in plots, the Braun-Blanquet scores were transformed to percentage cover values as follows: 5 = 87.5%, 4 = 62.5%, 3 = 37.5%, 2 = 15%, 1 = 2.5%, + = 1.0%, r = 0.02% (van der Maarel 1979). These values were considered as a measure of species abundance in a plot and included in the calculations of Shannon diversity and Pielou evenness.

The nomenclature of species was based on Pooley (1998), Schmidt *et al.* (2002), van der Walt (2009), and van Oudtshoorn (2012).

Table 1. Characteristics of the target invasive species. Data on the number of regions (at the scale of countries) where the species has naturalized (globally/African) are taken from the GloNAF database (Pyšek et al. 2017, van Kleunen et al. 2015). All species are annual and invasive in KNP (Foxcroft et al. 2023)

Species	Family	Origin	1 st KNP record	Regions naturalized
<i>Datura innoxia</i> Mill.	Solanaceae	Central America	1953	272/39
<i>Parthenium hysterophorus</i> L.	Asteraceae	American tropics	2003	119/13
<i>Xanthium strumarium</i> L.	Asteraceae	North America	1953	147/17

Univariate statistical analyses

Two types of data were used as importance values for the univariate analyses. First, data considering all species recorded in the herbal layer (including the target dominants and other aliens) were used to calculate species richness S , Shannon diversity H' , and Pielou evenness J . The same procedure was applied using data only for native species, i.e., excluding the target alien dominants and other aliens.

The Shannon diversity H' (Magurran 2004) was calculated as

$$H' = - \sum (P_i * \ln(P_i))$$

where P_i = relative abundance of species i . The Pielou evenness (Pielou 1966) was calculated as

$$J' = \frac{H'}{\ln(\text{species richness})}$$

Linear mixed-effect models (LMM, e.g., Raudenbush & Bryk 2002) were used to detect the pairwise differences between the invaded and uninvaded control plots. Species richness S , Shannon diversity H' , and Pielou evenness J were set as response variables in three separate LMM models; the invaded/uninvaded status of each plot and the target alien species' identity were the predictors. The site and pairs of invaded and uninvaded plots (nested in sites) represented the random effects, hierarchically arranged as follows: $m1 < \text{lme}(\text{richness or diversity or evenness} \sim \text{invaded-control plots} * \text{alien identity}, \text{random} = \sim 1 | \text{site/pair})$.

The same LMM models were used to test the differences in the richness of other alien species (besides the three target invaders *D. innoxia*, *P. hysterophorus*, and *X. strumarium*) present in invaded and uninvaded plots. Separate LMM models were used to test the effect of each of the three invaders: $m2 < \text{lme}(\text{richness or diversity or evenness} \sim \text{invaded-control plots}, \text{random} = \sim 1 | \text{site/pair})$.

LMM regression models and LMM analyses of covariance were used to test (i) the relations between the native and alien species richness and the dominant species' relative cover and (ii) the differences in these relations between the native and alien species. The relative cover was expressed as the ratio between the dominant's cover and the sum of the covers of species present in the herb layer of a given plot. In these models, the dominant's relative cover was the predictor, the species richness was the response variable, and the native vs. alien origin of species represented the factor variable in the analyses of covariance. The interaction term between the dominant's relative cover and species'

origin (native vs. alien) was of the most interest in the LMM analyses of covariance, as it represented the difference in the response of native and alien species to the invader's dominance. As in all LMM models, the sites and pairs of plots (nested in sites) were set as the random effects, hierarchically arranged. The script for the LMM analyses of covariance was: $m1 < \text{lme}(\text{species richness} \sim \text{dominants' relative cover} * \text{species' origin}, \text{random} = \sim 1 | \text{site/pair})$.

Square root and log transformations of the data were used to achieve normality, which was then tested using the Shapiro-Wilk normality tests (Crawley 2007). The arcsin transformation was applied to the relative dominant's cover. The accuracy of LMM models was inspected using the plots on the relations between the residuals and fitted values as well as by normal probability plots (Crawley 2007). All univariate models were created in the R software (R Development Core Team 2013) using the package nlme.

Multivariate statistical analyses

First, constrained ordinations were used to test the differences in species composition between the invaded plots and uninvaded control plots; the pair identity was set as a 'block defining covariable' (nested in 'site' and 'alien invader's identity' that were also included as covariables – see, e.g., Lepš & Šmilauer 2014). This arrangement ensured that the invaded and uninvaded plots were permuted within closely related pairs, filtering out the variability given by the differences between the three target aliens and the individual sites, as this variability was not considered interesting in relation to research hypotheses. Second, separate ordination models were used to test the compositional differences between the invaded vs. uninvaded vegetation for each invasive dominant (*D. innoxia*, *P. hysterophorus*, and *X. strumarium*). In these analyses, the pair identity was set as a 'block defining covariable' nested only in 'site'.

All species of the herb layer were included in the ordination analyses except the target aliens. Ordination analyses were performed twice: once with percentage covers of species as importance values to detect differences given by species abundances and then with binary presence/absence data to detect purely qualitative differences in species composition.

Results

Univariate analyses

In a model with the three target invaders analysed together, invaded plots harboured less species (both for all and native species only) than uninvaded plots: 21.5 ± 6.7 vs. 24.7 ± 8.2 , and 16.2 ± 5.9 vs. 19.6 ± 7.9 , respectively; $p = 0.011$ and $p = 0.001$ (Table 2, Supplementary Table 1). For individual species, the invasion of *P. hysterophorus* resulted in significant differences between invaded and uninvaded plots, both in terms of all (22.7 ± 5.8 vs. 29.5 ± 8.4 , $p = 0.038$) and native species richness (17.5 ± 5.2 vs. 25.3 ± 6.9 , $p = 0.009$). The differences in plots invaded by *D. innoxia* and *X. strumarium* and their controls were not significant (Figure 3).

Based on all data and the three invasive species merged, invaded plots showed lower Shannon diversity H' and Pielou evenness J than uninvaded plots: 1.04 ± 0.23 vs. 1.37 ± 0.60 , $p = 0.005$, and 0.35 ± 0.07 vs. 0.43 ± 0.17 , $p = 0.03$, respectively (Table 2, Supplementary Table 1). Among individual species, plots invaded by *P. hysterophorus* had significantly lower H' and J for all species than uninvaded plots: 1.09 ± 0.32 vs. 1.51 ± 0.24 , $p = 0.004$, and 0.35 ± 0.09 vs. 0.45 ± 0.07 , $p = 0.007$, respectively. The same was true for *D. innoxia* (0.99 ± 0.22 vs. 1.67 ± 0.71 , $p = 0.002$ and

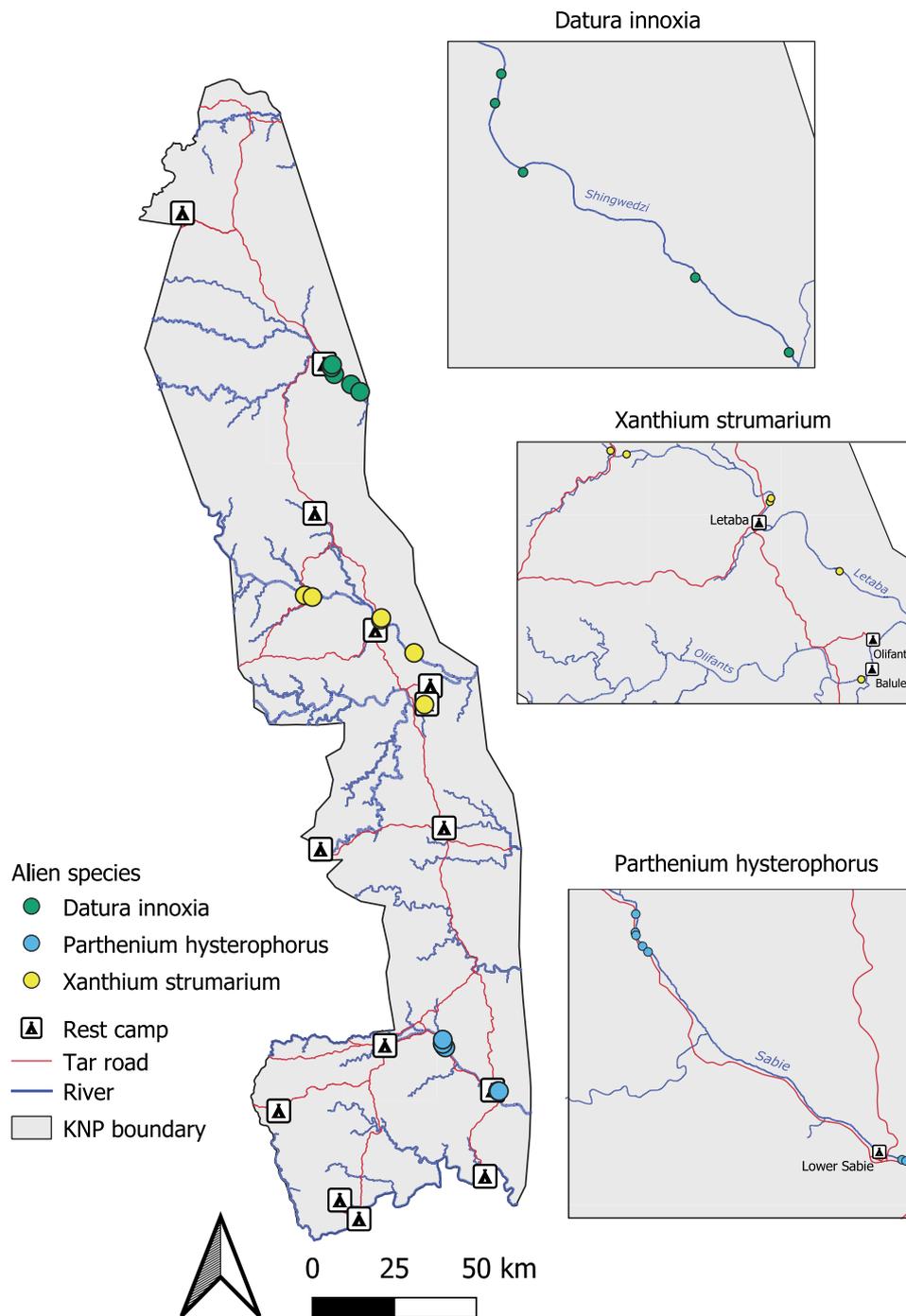


Figure 2. Location of study sites in the Kruger National Park. The *Datura innoxia* sites are indicated by red circles, *Parthenium hysterophorus* by yellow, and *Xanthium strumarium* by blue circles.

0.32 ± 0.06 vs. 0.52 ± 0.20 , $p = 0.003$, respectively). No significant differences in H' and J were found for *X. strumarium* (Figure 3).

On the contrary, invaded plots showed slightly higher Shannon diversity H' (1.22 ± 0.51 vs. 1.14 ± 0.58) and Pielou evenness J (0.44 ± 0.16 vs. 0.38 ± 0.17) for native species, compared to uninvaded plots in a model including all three invasive species, but the differences were not significant ($p = 0.880$ and $p = 0.505$, respectively).

No significant differences in the richness of alien species (with the target invaders excluded) were detected between the invaded and uninvaded plots, whether considering all three target invaders together or testing their effects separately.

However, alien and native species differed in their response to invaders' cover. If the species richness for both groups is regressed on the relative cover of the invader (expressed as the proportion of the total community cover it contributes, Figure 4), in a model with data for all three invaders merged, native species richness decreases ($T = -3.641$, $DF_{res} = 34$, $p = 0.001$) whereas the trend for alien species is not significant ($T = 1.104$, $DF_{res} = 34$, $p = 0.277$); this difference in the relationships for natives and aliens is marginally significant ($T = 1.935$, $DF_{res} = 72$, $p = 0.057$). With regard to particular species, *P. hysterophorus* is the only one with a significantly different relationship of alien and native species to its increasing cover ($T = 3.692$, $DF_{res} = 22$, $p = 0.001$).

Table 2. Results of univariate tests comparing species richness S , Shannon diversity H' and Pielou evenness J between the invaded and adjacent uninvaded (control) plots; n = the number of pairs with invaded plots and their controls, giving the number of replicates used in the respective tests. The differences among the subgroups of data (all species and native and alien separately) were tested using the LMM models, accounting for the autocorrelation of the data. Significant differences are in bold, marginally significant ($0.05 < p < 0.1$) in italics. The results indicate that, when comparing all invaded plots with adjacent uninvaded plots, the invaded plots show significantly lower species richness (S), lower Shannon diversity (H') and lower Pielou evenness (J)

Predictor	n	DF _{res}	S (all)		S (native)		S (alien)		H' (all)		H' (native)		J (all)		J (native)	
			T-value	p-value	T-value	p-value	T-value	p-value	T-value	p-value	T-value	p-value	T-value	p-value	T-value	p-value
invasion	37	34	2.686	0.011	3.560	0.001	-1.050	0.301	2.993	0.005	0.152	0.880	2.259	0.030	-0.673	0.505
alien	37	15	-1.279	0.220	-1.286	0.218	0.779	0.448	-0.651	0.525	-1.882	0.079	-0.785	0.445	-2.285	0.037
invasion × alien	37	34	-1.743	0.090	-2.326	0.026	1.113	0.273	-3.170	0.003	-0.749	0.749	-2.763	0.009	-0.724	0.474
<i>Datura innoxia</i>	12	11	1.221	0.248	0.605	0.385	0.711	0.492	4.203	0.002	-0.688	0.505	3.742	0.003	-1.165	0.269
<i>Parthenium hysterophorus</i>	12	11	2.364	0.038	3.140	0.009	-1.008	0.335	3.674	0.004	0.235	0.819	3.301	0.007	-1.389	0.192
<i>Xanthium strumarium</i>	13	12	0.579	0.573	0.873	0.400	0.183	0.858	-1.288	0.222	-0.676	0.512	-1.150	0.273	-1.406	0.170

Multivariate analyses

The composition of plots dominated by any of the three invaders significantly differed from that of adjacent uninvaded vegetation, both when species cover and binary presence/absence data were used as importance values in ordination analyses: $p = 0.002$ and $p = 0.002$, respectively (Table 3). Concerning the separate models on each of the invaders, their impacts on species composition were always significant, the only exception being that of *P. hysterophorus* when binary presence/absence data were used as importance values (Table 3). As shown by the ordination plots, the majority of native species are more abundant and frequent in the uninvaded vegetation (Figure 5), but some of them reach higher values of these characteristics in invaded than in uninvaded plots (Table 4).

Discussion

Differences in species richness, diversity and evenness

In general, the three target invaders show a negative impact on native vegetation, manifested by the differences between the invaded and adjacent uninvaded plots. At the level of individual species, *Parthenium hysterophorus* had a consistently negative impact on the species richness and diversity of the invaded community. The lowered species diversity by *P. hysterophorus* invasion was due to a decrease in species richness and evenness, with both characteristics contributing similarly to the diversity reduction. The invasion by *Datura innoxia* did not reduce species richness but had a strong negative impact on Shannon diversity, mediated by the markedly reduced evenness. For *Xanthium strumarium*, consistently across community characteristics and species groups (native or alien), we did not find evidence of impact.

All three species are very strong dominants, reaching up to 100% cover. The significant differences in Shannon diversity and evenness between invaded and uninvaded plots disappear if only native species are considered in analyses, and these community characteristics tend to be even higher than they are in the invader's presence, more so in *D. innoxia* invaded plots. This is because with a strong invasive dominant present, other species in the community are suppressed, and the probability of the occurrence of a strong native dominant is low. Once the strong invasive dominant is excluded from the calculation, both H' and J' reach the same or even higher values in invaded plots.

Differences in species composition

Besides the observed impact on the community characteristics, the three invaders significantly affected the frequencies with which other species occur and the abundances, proxied by the cover, that they reach. This is reflected in significant compositional differences between invaded and uninvaded plots; for *P. hysterophorus*, the effect was only obvious in analysis with species covers included, as covers use more information from the data and reflect the differences in abundances, whereas the tests on binary data reflect only qualitative changes in species composition. Yet, from the consistent impact on species composition, it follows that the majority of native species must react consistently to the invasion of any of the three dominant aliens by either decreasing or increasing their cover and frequency in the invaded vegetation. Most native species show a negative response to the invasive dominant, as revealed by the ordination plots. However, there are native species that are more frequent (*Abutilon ramosum*, *Bothriochloa radicans*,

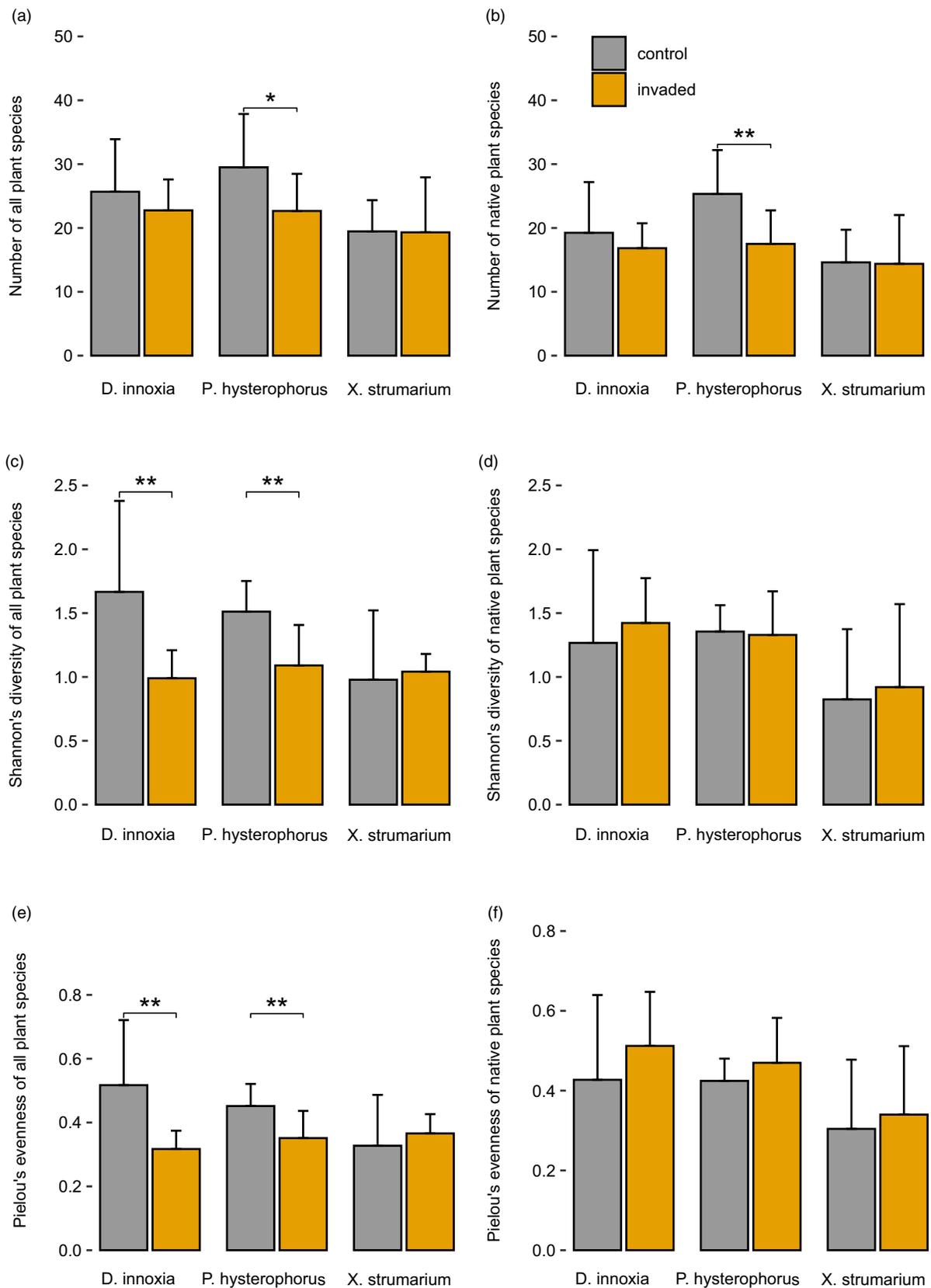
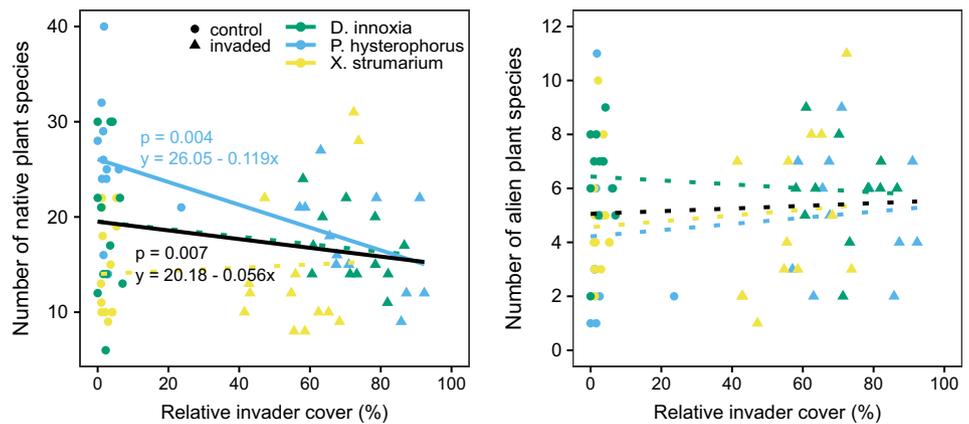


Figure 3. Differences in the number of species S , Shannon diversity H' , and Pielou evenness J between invaded and uninvaded (control) plots for the three alien invasive species studied. Bars show means and error bars standard deviation of the mean. Figures on the left side of the panel (a, c, e) show the differences for all species and those on the right (b, d, f) side only for the native plant species. Significant differences are marked with asterisks * $p < 0.05$, ** $p < 0.01$. The figure shows that of the three target invaders, *Parthenium hysterophorus* has the most pronounced negative impact on species richness. However, when considering all present species (i.e., including aliens), *Datura innoxia* has the most pronounced negative impact on Shannon diversity and Pielou evenness.

Table 3. Results of ordination analyses comparing the species composition of invaded and uninvaded plots, using species percentage covers and presence/absence (binary) as input data. The percentage of explained variation is given, and significant results are in bold. The results are shown for all invasive species and each species individually to indicate how much they affect the species composition

Predictor	Cover		Binary	
	Variation (%)	<i>p</i> -value	Variation (%)	<i>p</i> -value
All invasives	7.0	0.002	4.1	0.002
<i>Datura innoxia</i>	14.4	0.002	10.5	0.028
<i>Parthenium hysterophorus</i>	11.8	0.026	10.0	0.106
<i>Xanthium strumarium</i>	11.3	0.002	9.7	0.012

Figure 4. Relationship between the numbers of native and alien species in 10 × 10 m plots, and the relative cover of the three invasive species, expressed as the contribution of its cover to the total cover in the plots. Invaded and control plots are marked by different symbols and the target invaders by different colours. Regression lines are based on simplified linear models including only the predictor and response variable; significant relationships are indicated by solid lines, nonsignificant by dotted lines. The trend based on data for all three invaders merged is indicated by the black line.



Cyperus rupestris, *Grewia villosa*) or more abundant in the invaded vegetation (*Abutilon ramosum*, *Coccinia rehmani*, *Panicum deustum*, *Ruellia cordata*).

Contrasting ecologies drive impact mechanisms

All three species targeted by our study are noxious invaders not only in Africa but also on a global scale. Their naturalized populations have been recorded in 17–32% of regions of the world, based on the GloNAF database (Pyšek *et al.* 2017, van Kleunen *et al.* 2015, 2019). More importantly, their impacts have been reported in many regions (Holm 1997, Weber 2017). This is especially true for *P. hysterophorus*, which has been shown to alter soil nutrient composition and displace native plant species through competition and allelopathy in a wide range of habitats (Adkins & Shabbir 2014, Matzrafi *et al.* 2021) and therefore represents the greatest threat to KNP riparian areas (e.g., Bajwa *et al.* 2019, Brunel *et al.* 2014, Chhogyel *et al.* 2021, Timsina *et al.* 2011). Yet, the impact on the richness and diversity of other species in our system, although overall significant and detectable, varied among the invaders and with regard to the community characteristics used to measure it.

When drawing conclusions about what these invasions mean for savanna vegetation, it needs to be borne in mind that the magnitude of impact detected depends on the scale of sampling (Stohlgren *et al.* 2002). In our study, because we were interested in recording the effect the invasive dominants have in a broader landscape context, we focused on the community scale, using plots of the size commonly used to study herb vegetation layer (Chytrý *et al.* 2008, Stohlgren *et al.* 2006). With increasing scale, the

impacts may become less pronounced because other species in invaded communities can survive or newly colonize by utilizing the gaps in the invader's cover, a mechanism that we observed in the field. This is also an explanation, at least in part, for the differences in the severity of impacts among the invaders studied. The observed impact of *Parthenium hysterophorus* was generally the most pronounced of the three, and at the time of sampling, this species created the densest populations with very little space for other species once it reached a high cover; interestingly, it has been suggested that *P. hysterophorus* has an allelopathic potential (Singh *et al.* 2003, van der Laan *et al.* 2008) that was not reported for the other two invaders. At the time of sampling, the stands of *X. strumarium* and *D. innoxia* were usually patchy, and even if having a high cover, their growth habit provides space for other species on patches of bare ground and lower in the stand – this made the impact of these two species less pronounced.

The differences in the ecology of particular invaders further contribute to the variation in the severity of impacts that we recorded. As *P. hysterophorus* invades the shrubby savanna and clearings in gallery forest higher at the river edge, it often replaces species-rich grassy savanna (Figure 1f). Hence, the loss of species due to invasion is generally more pronounced compared to other two invaders that replace vegetation that is poorer in species (Figure 3a and b), such as the sandy river channel floor (Figure 1b) or grazing lawns (Figure 1h). There, the invasion often creates patches of different substrates, clayey and richer in nutrients, with plant remnants, seeds, soil, and debris brought by the river flow. Such places provide suitable habitats to ruderal species with higher demands for nutrients, facilitating their colonization of invaded sites (Figure 1a), thereby reducing the impact of *D. innoxia* and

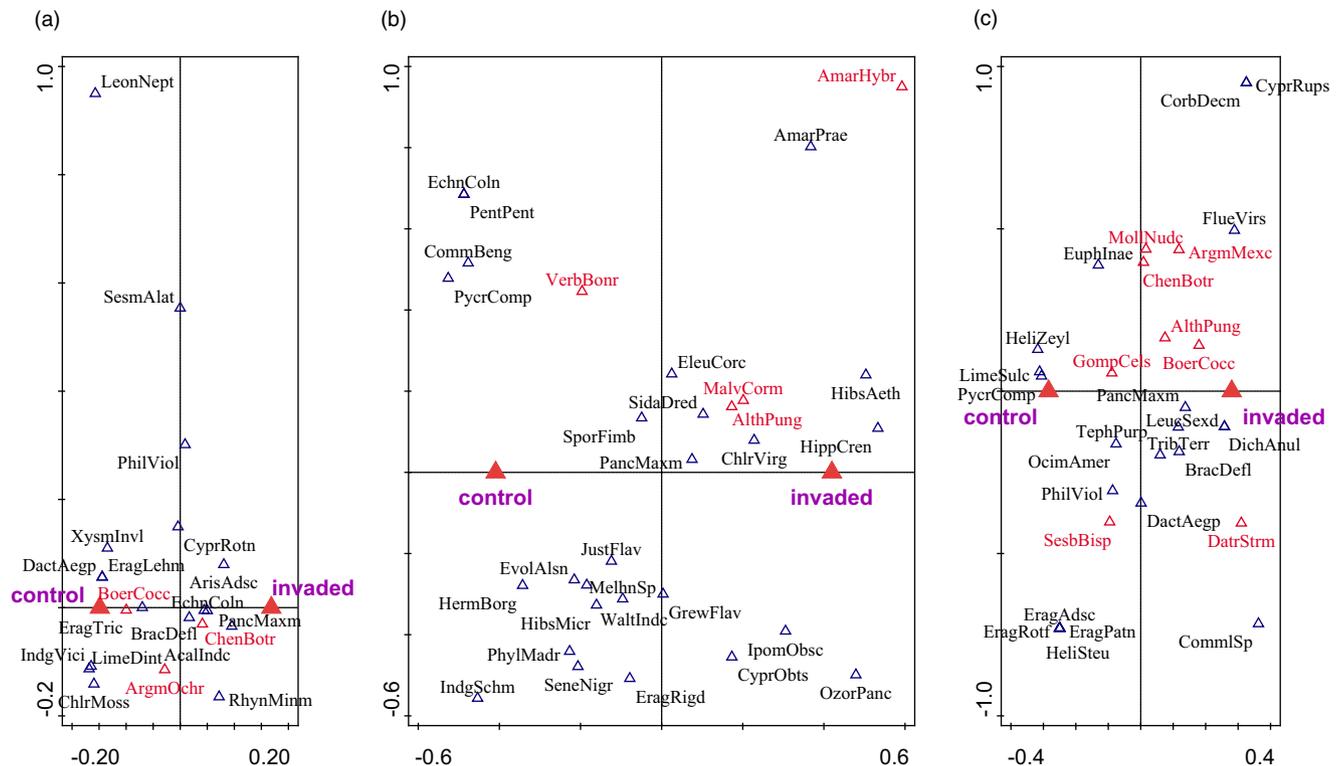


Figure 5. Ordination plot showing the compositional differences between the invaded and uninvaded plots for *Datura innoxia* (a), *Parthenium hysterophorus* (b) and *Xanthium strumarium* (c). Binary (presence-absence) data were used as importance values. The locality and pair (nested in locality) were included as covariables; the pair of invaded and uninvaded plots was set as a 'block defining covariable'. Abbreviations: SeneNigr = *Senegalia nigrescens*, AcalIndc = *Acalypha indica*, AlthPung = *Althermanthera pungens*, AmarHybr = *Amaranthus hybridus*, AmarPrae = *Amaranthus praetermissus*, AristAdsc = *Aristida adscensionis*, ArgmMex = *Argemone mexicana*, ArgmOchr = *Argemone ochroleuca*, ArsCong = *Aristida congesta*, BercDisc = *Berchemia discolor*, BoerCocc = *Boerhavia coccinea*, BracDefl = *Brachiaria deflexa*, BulbHisp = *Bulbostylis hispidula*, ChenAmbr = *Chenopodium ambrosioides*, ChenBotr = *Chenopodium bothrys*, ChlrMoss = *Chloris mossambicensis*, ChlrVirg = *Chloris virgata*, CleoAngs = *Cleome angustifolia*, CombMoss = *Combretum mossambicense*, CommBeng = *Commelina bengalensis*, CommErec = *Commelina erecta*, CorbDecm = *Corbichonia decumbens*, CucmZeyh = *Cucumis zeyheri*, CyprObts = *Cyperus obtusiflorus*, CyprRotn = *Cyperus rotundus*, CyprRups = *Cyperus rupestris*, CyndDact = *Cynodon dactylon*, CyprSexn = *Cyperus sexangularis*, DactAegp = *Dactyloctenium aegyptium*, DactAust = *Dactyloctenium australe*, DatrStrm = *Datura stramonium*, DichAnul = *Dichanthium anulatum*, DichCinr = *Dichrostachys cinerea*, EchnColn = *Echinochloa colona*, EleuCorc = *Eleusine coracana*, EragAdsc = *Eragrostis adscensionis*, EragCili = *Eragrostis ciliaris*, EragLehm = *Eragrostis lehmaniana*, EragPatn = *Eragrostis patentipilosa*, EragRigd = *Eragrostis rigidior*, EragRotf = *Eragrostis rotifer*, EragSupr = *Eragrostis superba*, EragTric = *Eragrostis trichophora*, EuphHirt = *Euphorbia hirta*, EuphInae = *Euphorbia inaequilatera*, EvolAlsn = *Evolvulus alsinoides*, FelcMoss = *Felicia mossamedensis*, FlueVirs = *Flueggea virosa*, GompCels = *Gomphrena celosioides*, GrewFlav = *Grewia flavescens*, HeliSteu = *Heliotropium steudneri*, HeliZeyl = *Heliotropium zeylanicum*, HermBorg = *Hermannia boraginiflora*, HibsAeth = *Hibiscus aethiopicus*, HibsMicr = *Hibiscus micranthus*, HippCren = *Hippocratea crenata*, IpomObsc = *Ipomoea obscura*, IpomSine = *Ipomoea sinensis*, IndgCost = *Indigofera costatum*, IndgSchm = *Indigofera schimperferi*, JustFlav = *Justicia flava*, JustMatm = *Justicia matamensis*, IndgVici = *Indigofera vicioides*, KyphAngs = *Kyphocarpa angustifolia*, LeonNept = *Leonotis nepetifolia*, LeucSexd = *Leucas sexdentata*, LimeDint = *Limeum dinteri*, LimeSulc = *Limeum sulcatum*, LippJavn = *Lippia javanica*, MalvCorm = *Malvastrum coromandelianum*, MelhAcum = *Melhantha acuminata*, MelhSp = *Melhantha sp.*, MollNudc = *Mollugo nudicaulis*, OcimAmer = *Ocimum americanum*, OzorPanc = *Ozoroa paniculosa*, PancMaxm = *Panicum maximum*, PentPent = *Pentodon pentandrus*, PhilViol = *Philenoptera violacea*, PhylMadr = *Phyllanthus maderaspatensis*, PlucDios = *Pluchea dioscoridis*, PycrComp = *Pycnopus compressus*, RhynMinm = *Rhynchosia minima*, SesbBisp = *Sesbania bispinosa*, SesmAlat = *Sesamum alatum*, SidaDred = *Sida dredgei*, SprAfr = *Spirostachys africana*, SporFimbr = *Sporobolus fimbriatus*, SporLocl = *Tephrosia purpurea*, TragBert = *Tragus berteronianus*, TribTerr = *Tribulus terrestris*, TricMonc = *Tricholaena monachme*, TridProc = *Tridax procumbens*, UrocMoss = *Urochloa mossambicensis*, UrocOlig = *Urochloa oligotricha*, VerbBonr = *Verbena bonariensis*, WaltIndc = *Waltheria indica*, XysmInvl = *Xysmalobium involucreatum*, ZinnPerv = *Zinnia peruviana*. Alien species codes are shown in red font.

X. strumarium and further strengthening the differences among invaders in the magnitude of their impacts.

In terms of invasion theory, the observed mechanism points to the fertility islands described by Novoa *et al.* (2021) for KNP (i.e., the presence of alien plants might create favourable conditions for the establishment and growth of other plants) and can be interpreted as an indication of invasional meltdown (Braga *et al.* 2018, Simberloff & Von Holle 1999) – because the mechanism acts more effectively for alien species; it is thus not a 'ruderal meltdown' alone. This claim is supported by the result of the analysis of the relationship between invaders' covers and the occurrence of other species – high cover of invasive species reduced the native species richness (in line with other results, this was most pronounced for *P. hysterophorus*) but had no negative impact on alien species occurring in the plant communities sampled, rather the opposite trend was indicated (Figure 4).

Impact on vegetation and beyond: implications for management

The species selected provided a suitable model system to infer about different ecologies of invaders and hence mechanisms of invasion. All are annuals from the Americas, which makes species-specific biases, such as those associated with the region of introduction or with different life histories, irrelevant. On the other hand, while all target species spread along rivers, field experience suggests that they differ in their capacity to colonize areas outside riverbeds. *Datura innoxia* is most closely confined to sandy substrates in riverbeds, where *X. strumarium* is also common; the two species often occur together in invaded stands or in close proximity to each other. However, the latter species also invades riverbanks higher above the riverbed with more compact soils, and

Table 4. Lists of 10 species that were more represented in either the invaded vegetation or uninvaded control plots. Results are presented for the two types of data, presence/absence (binary) and species covers. Alien species are marked by an asterisk. The ranking of species is based on the ordination scores, expressing the likelihood of a species being more frequent or reaching higher covers in invaded or uninvaded vegetation. Therefore, the ranking does not reflect the most frequent (measured by presence) or abundant (measured by cover) species in absolute terms, but those whose performance between invaded and uninvaded plots differed most, and each species can only be listed in one type of plots where its performance was better

Invaded		Uninvaded (control)	
Presence/absence	Species cover	Presence/absence	Species cover
<i>Abutilon ramosum</i>	<i>Abutilon ramosum</i>	<i>Setaria pumila</i>	<i>Cleome angustifolia</i>
<i>Grewia villosa</i>	<i>Grewia villosa</i>	<i>Limeum sulcatum</i>	<i>Tricholaena monachne</i>
<i>Bothriochloa radicans</i>	<i>Setaria sagittifolia</i>	<i>Ageratum houstonianum*</i>	<i>Chloris mossambicensis</i>
<i>Sorghum versicolor</i>	<i>Ruellia cordata</i>	<i>Combretum macrophyllum</i>	<i>Tridax procumbens*</i>
<i>Justicia matamensis</i>	<i>Panicum deustum</i>	<i>Heliotropium zeylanicum</i>	<i>Vachellia nilotica</i>
<i>Urochloa repens</i>	<i>Achyranthes aspera*</i>	<i>Euphorbia minima</i>	<i>Zaleya pentandra</i>
<i>Cyperus rupestris</i>	<i>Coccinia rehmani</i>	<i>Dicoma tomentosa</i>	<i>Polygala amatymbica</i>
<i>Hippocratea crenata</i>	<i>Hybanthus enneaspermus</i>	<i>Aristida congesta</i> subsp. <i>barbicollis</i>	<i>Mollugo nudicaulis*</i>
<i>Ruellia cordata</i>	<i>Leucas sexdentata</i>	<i>Cleome angustifolia</i>	<i>Tricliceras glanduliferum</i>
<i>Digitaria notata</i>	<i>Cyperus rupestris</i>	<i>Tricholaena monachne</i>	<i>Indigofera vicioides</i>

P. hysterothorus is the most widespread of the three beyond riverbeds, commonly invading the understory of the gallery forest and clearings there. The ecology of all three invaders makes the comparison of invaded and uninvaded plots more robust as some of the cautions with regard to the space-for-time substitution approach (see Hejda *et al.* 2009 for discussion) are less relevant in places where rather large areas of homogeneous habitats in terms of substrate, dispersal opportunities, and disturbance regimes can be found to locate plots. The main potential limitation of the space-for-time approach is the uncertainty in the causality of the observed effects. In our case, the question might arise if the differences between invaded and control plots are really caused by the dominance of the target aliens or by a difference in some confounding factor, which may either promote or suppress the dominance of invading aliens. However, the stands of all three target aliens were spread over large homogenous riparian areas, which makes the presence of confounding factors unlikely. Moreover, a biased significant result would presume there are systematic rather than random differences between the invaded and control plots, which is also unlikely.

From a broader perspective, it needs to be emphasized that in a protected area such as KNP, the biodiversity conservation objectives aim “to maintain the delivery of broad ecosystem services by ensuring its biota and associated terrestrial processes are restored and maintained” (KNP 2018). When studying the impacts of invasive plant species, the focus needs to be on the whole ecosystem and consider other potential ecosystem impacts, such as on herbivores (Pyšková *et al.* 2022a), other animals (Foxcroft *et al.* 2022), and soils (Novoa *et al.* 2021). Such an approach allows us to gain a holistic understanding of invasion impacts and provide a complete assessment of management needs. Here, we examined the effects of three invasive alien plants on one aspect of a larger programme, namely, impacts on vegetation. Our results show that the invasions of two of the target aliens (*Datura* sp. div., *X. strumarium*) are unlikely to have profound effects on the diversity of the riverbed vegetation. However, there is evidence that they still have significant compositional effects. A study on the effects of management and post-control response of invasive alien plants in the KNP (Morris *et al.* 2008) suggested that continuous

control of riparian alien species, including *X. strumarium*, would reduce seed production and limit the displacement of recovering native vegetation, allowing natural rehabilitation. However, with the introduction of *X. strumarium* in 1953, any reduction in seed production is likely to have little effect at this point. *Parthenium hysterothorus*, which also spreads outside of the river channel, both reduces overall plant diversity and changes species composition.

When suggesting management policies, the feasibility of achieving the objectives, including the likelihood of success and costs of control, also needs to be considered in addition to their impacts. All management measures need to be designed with the awareness that complete eradication from KNP of these invasive species is impossible. For this reason, it may be necessary to accept the presence of stands of *Datura* sp. div. and *X. strumarium* in the riverbeds for part of the year, as being annual species, they die at the end of summer. According to van Wilgen *et al.* (2017), much funding has been spent on *X. strumarium* control, with little long-term success. Also, populations of these aliens re-establish rapidly following control. Should the species be found to be invading other areas where there is a higher likelihood of impacts on diversity, management would be recommended. It needs to be noted, however, that these recommendations are based on vegetation impacts, while the impacts on other ecosystem components may enhance the need for control. However, *P. hysterothorus* deserves special attention due to its stronger impacts and direct competition with co-occurring plant species, especially as it successfully invades outside the riverbeds along the macrochannel bank and in drainage lines or moist areas further away from rivers.

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