

Into the great wide open: do alien plants spread from rivers to dry savanna in the Kruger National Park?

Petr Pyšek^{1,2,3}, Martin Hejda¹, Jan Čuda¹, Guin Zambatis⁴, Klára Pyšková^{1,2}, Sandra MacFadyen⁵, David Storch^{2,6}, Robert Tropek^{2,7}, Llewellyn C. Foxcroft^{4,3}

1 Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43 Průhonice, Czech Republic **2** Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic **3** Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Matieland 7602, South Africa **4** Scientific Services, South African National Parks, Private Bag X402, Skukuza 1350, South Africa **5** Biodiversity Informatics Unit, Department of Mathematical Sciences, Stellenbosch University, Matieland 7602, South Africa **6** Center for Theoretical Study, Charles University, Jilská 1, CZ-110 00 Prague, Czech Republic **7** Institute of Entomology, Biology Centre, Czech Academy of Sciences, České Budějovice, Czech Republic

Corresponding author: Petr Pyšek (pysek@ibot.cas.cz)

Academic editor: Sven Jelaska | Received 22 May 2020 | Accepted 22 July 2020 | Published 18 August 2020

Citation: Pyšek P, Hejda M, Čuda J, Zambatis G, Pyšková K, MacFadyen S, Storch D, Tropek R, Foxcroft LC (2020) Into the great wide open: do alien plants spread from rivers to dry savanna in the Kruger National Park? NeoBiota 60: 61–77. <https://doi.org/10.3897/neobiota.60.54608>

Abstract

Protected areas play an important role as refuges from invasive species impacts on biodiversity. Within the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project, plant species were recorded in a representative set of 60 plots, 50 × 50 m in size, across the entire KNP, distributed so as to cover a range of savanna habitats, i.e. perennial rivers, seasonal rivers and dry crests, and two main bedrock types (granite and basalt). The data were used to assess the role of rivers in the dispersal of alien plants and study whether the alien plant species spread from rivers to open dry savanna. The resulting dataset provided the first thorough information on the spatial distribution of naturalised alien plants in KNP. In total, we recorded 20 plant species that are alien to the park, four of them considered invasive: *Parthenium hysterophorus*, *Opuntia stricta*, *Xanthium strumarium* and *Zinnia peruviana*. The most widespread species in KNP was *Tridax procumbens*, recorded in 11 plots (i.e. 18% of all sampled), four other species were found in > 10% of the plots. One species, *Bidens bipinnata*, was not previously reported from the park and represents a new record. The majority of aliens were concentrated along perennial rivers (60% of all occurrences), but some were repeatedly recorded at seasonal rivers as well and two of the most invasive species in KNP, *Opuntia stricta* and *Parthenium hysterophorus*, occurred also on dry crests away from water.

The average number of alien species per plot was low (1.6), as was their mean percentage contribution to all species in a plot (2.2%), but some plots harboured as many as seven species and contributed up to 11.9%. Moreover, only 21 plots (35%) were alien-species free. In terms of the total species number per habitat, perennial rivers had significantly more aliens than crests and were marginally significantly richer than seasonal rivers. By recording all naturalised alien species occurring in the plots – many of them are not invasive but may become so in the future – and by using the GloNAF database of global distribution of naturalised species, we assessed the invasion potential of the recorded species.

Keywords

alien species richness, crest, habitat, perennial river, plant invasion, protected area, savanna, seasonal river

Introduction

The majority of protected areas worldwide are vulnerable to invasions, with very few completely free of alien species (Foxcroft et al. 2017; Moodley et al. 2020) and many suffering various impacts at the species and community levels. These impacts include the alteration of habitats, ecosystem regime shifts and losses to native species abundance, diversity and richness (Foxcroft et al. 2013; Hulme et al. 2014; Pyšek et al. 2020). In a global assessment, De Poorter (2007) found there were 487 protected areas where invasive alien species posed a serious threat to biodiversity. Along these lines, invasive plants are almost universally regarded as a major threat by managers of protected areas (Pyšek et al. 2013). However, the situation is not improving over time, as shown by Shackleton et al. (2020). These authors compared how the threat by and management of invasive species have changed in a representative set of 21 protected areas that were included in the international SCOPE programme on biological invasions in the mid-1980s (Drake et al. 1989). Amongst the taxonomic groups analysed, invasive plants pose the greatest continued threat, as documented by increased numbers in 31% of the protected areas over ~30 years from 1980s to the present (Shackleton et al. 2020).

One of the iconic protected areas included into the SCOPE programme is the Kruger National Park (KNP) in South Africa. Established in 1898, it is the largest game reserve in South Africa and one of the oldest national parks in the world (Caruthers 1995). It covers an area of ~20,000 km², the majority in a subtropical climate with the Tropic of Capricorn crossing the park in the North. Several large, mostly perennial, rivers flow through the park in a west-east direction, including Sabie, Olifants, Crocodile, Letaba, Shingwedzi, Luvuvhu and Limpopo (Fig. 1, MacFadyen et al. 2018). Environmental heterogeneity is generated by a mosaic of geological conditions (granitoid bedrock in the western vs. basalt and gabbro in the eastern part), altitude (140–780 m a.s.l.), climate (450–750 mm of annual precipitation) and character of vegetation (dominant woody species, proportional representation of woody cover vs. open grassland; du Toit et al. 2003; MacFadyen et al. 2016).

There are about 360 alien plant species currently recorded in KNP (Foxcroft et al. 2017), of which only a few are considered noxious invaders (Jarošík et al. 2011).

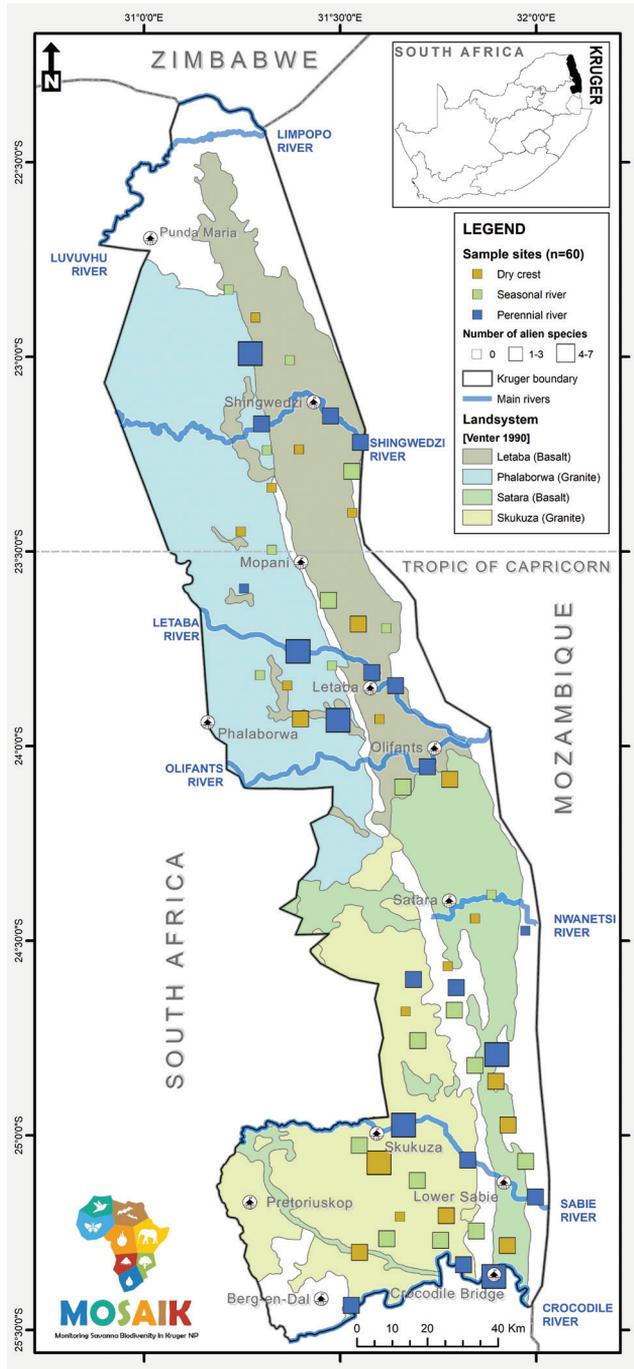


Figure 1. The Kruger National Park situated between latitudes 22°19'40"S to 25°31'44"S and longitudes 30°53'18"E to 32°01'59"E, with location of the 60 sampled sites, separated according to habitat and distributed across the four land systems. The size of the symbols indicates the number of alien plant species recorded in the plot.

The boundaries of KNP were shown to act as a barrier to invasions from the surrounding intensively-used agricultural landscape or urbanised areas (Foxcroft et al. 2011), in accordance with the role protected areas play in other parts of the world by offering refuges from invasive species (Pyšek et al. 2003; Gallardo et al. 2017). For KNP, it has been shown that the best human-related predictors of the number of alien invasive plants inside the park were the amount of water bringing propagules from adjacent densely populated areas, together with density of major roads (Foxcroft et al. 2011) and human settlements in the park surroundings (Spear et al. 2013). A study of invasive species across South African National Parks identified ornamental planting and rivers as the primary pathways of invasion (Foxcroft et al. 2019) – a large number of alien ornamental species and alien species occurring along rivers are reported for KNP (Foxcroft et al. 2008). Therefore, a great threat from alien plant invasions to KNP is associated with rivers that act as the most efficient pathways for propagules from adjacent areas. However, while these indicators represent the potential for introduction of alien plants into KNP, the context dependence of the invasion process requires study at finer scales to determine which alien species may become naturalised and invade within KNP.

In response to the escalating importance of plant invasions, KNP has initiated a number of programmes aimed at preventing and mitigating incursions of alien species (van Wilgen et al. 2017). These efforts have yielded data on the distribution of major invaders through long-term monitoring (Foxcroft et al. 2009) and species-specific studies on the ecology of particular invaders (Foxcroft et al. 2004; Hui et al. 2011). However, as is often the case in plant invasion research, the data collection focused on alien species hotspots, such as human-disturbed habitats or rivers and, to date, none of the projects in KNP has systematically investigated the distribution of alien plants across the entire park or assessed how successfully they persist across a range of different habitats.

To contribute to closing this gap, we use our data collected by the MOSAIK (Monitoring Savanna Biodiversity in the Kruger National Park) project aimed at studying biodiversity across the entire KNP, within four distinct land systems with variable supply of water and contrasting geologies. Here we aim to (i) describe the distribution of alien plant species, (ii) assess to what extent alien plants are confined to rivers as the main introduction pathways and dispersal vectors, versus how commonly they occur in drier habitats away from rivers and (iii) identify potentially invasive species of the future.

Methods

Data collection

The data analysed in this paper were collected within the MOSAIK project between 2018 and 2020. MOSAIK's primary objective is to sample plant and animal (mammals, birds, bats and moths) biodiversity in habitats across different land systems in

KNP (as defined by Venter 1990). To this purpose, we established triplets of 50×50 m plots, each triplet including a site (i) near a perennial river or another permanent source of water, such as a dam or pool (the criterion being water present all year round), (ii) near a seasonal river, defined as a river or stream where water is only present in the rainy season and (iii) on a dry crest at least 5 km from any source of water (Fig. 2). The plots within each triplet were selected to capture the different habitats in a similar landscape context within a reasonable distance of ~7–13 km between plots. There were 20 triplets distributed so as to cover the four land systems (five triplets in each), giving a total of 60 plots (Fig. 1). Consequently, each of the three habitats was sampled by 20 plots and each of the two bedrock types by 30 plots.

Plants were sampled during two rainy seasons, 16 January to 4 February 2019 and 17 January to 3 February 2020. All vascular plant species were recorded in each 2500 m² plot and their abundance estimated visually using the Braun-Blanquet cover-abundance seven-grade scale (Mueller-Dombois and Ellenberg 1974). To quantify the occurrence of species in plots, the Braun-Blanquet scores were transformed to percentage 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). The time spent to sample a plot ranged from 1 to 7 hours, with an average of $2:15 \pm 1:01$ hour (mean \pm S.D.).

Species that are alien to South Africa were selected for analyses in this paper. To assign species an alien status, we followed geographical criteria broadly accepted in the invasion literature, referring to species introduced by humans to regions outside their native range (see Pyšek et al. 2004; Essl et al. 2018 for definitions). Further, to classify which of the recorded alien species are naturalised (forming self-sustainable populations in the wild) or invasive (subgroup of naturalised species rapidly spreading in the invaded area), we followed the definition proposed by Richardson et al. (2000) and Blackburn et al. (2011). This classification of species was based on previous publications relevant to the study area (Foxcroft et al. 2017). For each species, we recorded the region of origin and life history information.

To assess the invasion potential of the alien species recorded in KNP, we extracted information on their global naturalisation success from the GloNAF (Global Naturalized Alien Flora) database (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). This database includes information on the occurrence of naturalised plant species in 843 regions of the world (at the level of countries, states and provinces in case of large countries and islands) and summarises the distributions of almost 14,000 taxa. For each species recorded in our plots, we extracted the number of GloNAF records globally and in Africa.

Statistical analysis

Differences amongst habitats and bedrock in the mean numbers of alien species in plots were tested by using a Linear Mixed-Effects Model (LMM) (R Development Core Team 2013; Bates et al. 2015). The square-root of the number of alien species

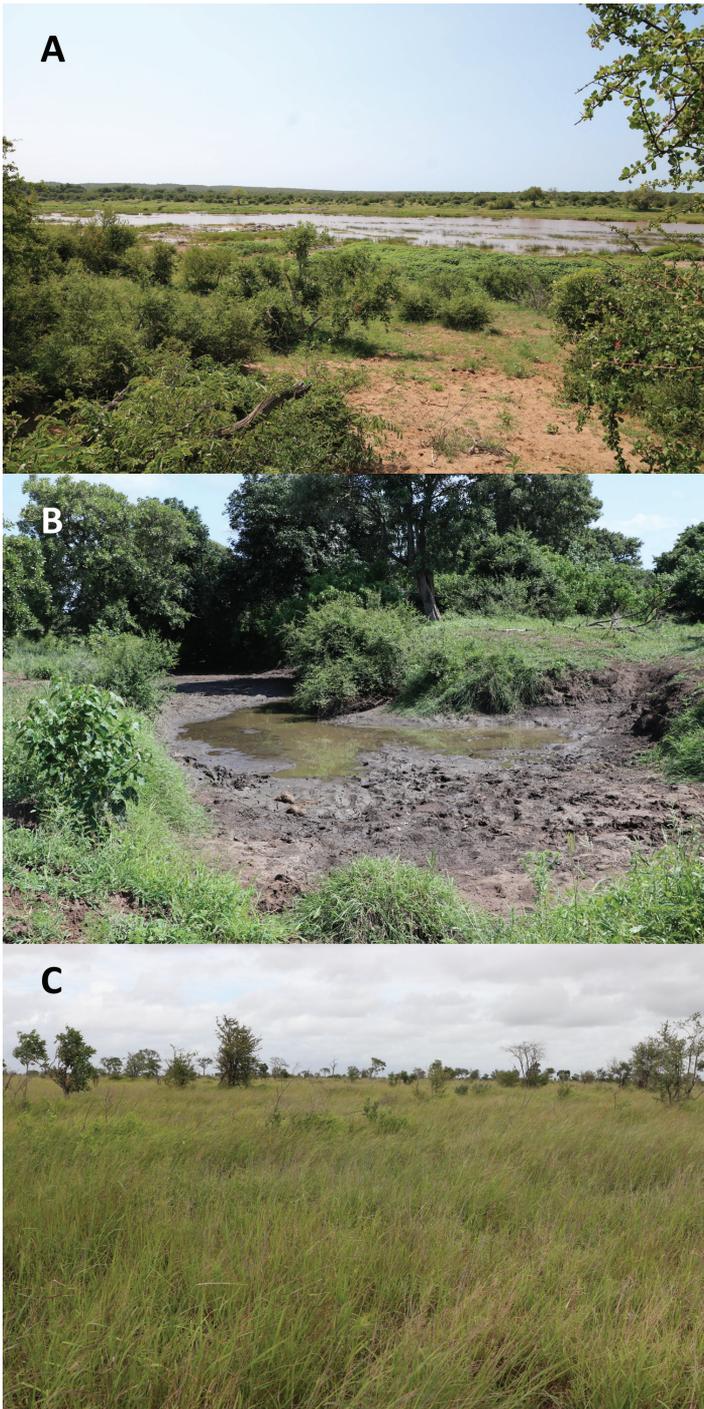


Figure 2. Images of habitats that were considered in the Kruger National Park study: **A** perennial river, **B** seasonal river and **C** dry crest. The plots were located in the vicinity of the rivers, near the river beds and within the crest.

was the response variable and the type of bedrock (granite vs. basalt), habitat (seasonal rivers, perennial rivers, crests) and their interactions were the predictors. The triplets of plots were set as the random effect factor (grouping variable). Possible autocorrelations, based on the distances between individual triplets, were modelled as a continuous function, using the “cor” parameter. The significances of different predictors (bedrock, habitat, bedrock × habitat interaction) were tested using deletion tests, by comparing the explanatory power of models with and without a particular term (Crawley 2007). The quality of models was checked visually, by plotting standardised residuals against fitted values. Possible deviations from normality were inspected using probability plots. The data on the percentages of aliens amongst all species in plots were arcsin-transformed.

A log-linear model (Crawley 2007) was used to test the differences in the total numbers of aliens amongst different habitats and bedrocks. In this model, the total number of aliens was the response variable and habitat (seasonal rivers, perennial rivers, crests), bedrock (granite, basalt) and their interaction were the predictors. The significance of individual terms was tested using deletion tests, by comparing the explanatory power of models with and without that particular main effect or interaction (Crawley 2007). All models were created in the R software (R Development Core Team 2013).

Results

Structure of alien flora: effects of habitat and bedrock on species' occurrence patterns

In total, we recorded 20 plant species that are classified as naturalised aliens to KNP (Table 1). Family Asteraceae was most represented with nine species, followed by Amaranthaceae with four species, Cactaceae with two species and the remaining five species in five other families. There are 13 species that occur as annuals (50%), 10 as perennials (39%), two as shrub or semi-shrub (*Malvastrum coromandelianum* and *Datura innoxia*, respectively). Four of the species recorded are considered invasive in KNP: *Parthenium hysterophorus* (recorded in nine plots, i.e. 15% of all sampled), *Xanthium strumarium* (three plots), *Opuntia stricta* (three plots) and *Zinnia peruviana* (two plots). The remaining species are considered naturalised, except *Bidens bipinnata* that was not previously reported from the park and represents a new record; for this species, the status remains to be confirmed.

The most widespread species in KNP was *Tridax procumbens*, recorded in 11 plots (i.e. 18%), other species recorded in more than 10% of plots being *Bidens biternata*, *Malvastrum coromandelianum*, *Parthenium hysterophorus* and *Alternanthera pungens* (Table 1; Fig. 3). The majority of alien species recorded in our KNP plots have successfully naturalised in various parts of the world, with 11 of them occurring in more than 100 regions globally (*Portulaca oleracea* and *Chenopodium album* with 311 and 298 regions, respectively, are the most widespread). These data indicate the overall potential of recorded alien plants to spread; the majority of them have also successfully

Table 1. Overview of alien plant species recorded in savanna habitats in the Kruger National Park. Total number of records, separately for basalt and granite bedrock, frequency of occurrence in plots ($n = 60$) and the range of covers are given (one cover value indicates that the species occurred in plots with the same cover). Species that are currently considered as invasive in KNP are marked with * (based on Foxcroft et al. 2017). The naturalisation success is expressed as the number of regions in the GloNAF 1.1 database ($n = 843$, van Kleunen et al. 2015, 2019; Pyšek et al. 2017) in which the species is recorded as naturalised, shown globally and for Africa. Life history: a – annual herb, p – perennial herb, ss – subshrub. Species are ranked by decreasing frequency in KNP.

Species	Family	Life history	Origin	Occurrences	Frequency (%)	Basalt	Granite	Cover (%)	Naturalised (globally/in Africa)
<i>Tridax procumbens</i>	Asteraceae	a	central America	11	18.3	3	8	0.1	146/55
<i>Bidens biternata</i>	Asteraceae	a	East Asia (Himalayas)	10	16.7	4	6	0.1–15.0	31/29
<i>Malvastrum coromandelianum</i>	Malvaceae	a, p, ss	North America	10	16.7	5	5	0.1	161/29
<i>Parthenium hysterophorus</i> *	Asteraceae	p	North America	9	15.0	4	5	0.1	119/13
<i>Alternanthera pungens</i>	Amaranthaceae	p	tropical America	8	13.3	5	3	0.1–2.5	124/35
<i>Bidens bipinnata</i>	Asteraceae	a	Asia, North America	6	10.0	2	4	0.1–15	88/26
<i>Gomphrena celosioides</i>	Amaranthaceae	a, p	tropical South America	6	10.0	2	4	0.1	94/43
<i>Acanthospermum hispidum</i>	Asteraceae	a	tropical America	5	8.3	3	2	0.1–2.5	128/49
<i>Portulaca oleracea</i>	Portulacaceae	a	Eurasia	4	6.7	3	1	0.1	311/56
<i>Melanthera scandens</i>	Asteraceae	p	tropical to subtropical Africa	4	6.7	3	1	0.1	12/12
<i>Litogyne gariepina</i>	Asteraceae	p	obscure	3	1.7	2	1	0.1	–
<i>Xanthium strumarium</i> *	Asteraceae	a	America ¹	3	5.0	2	1	0.1	147/18
<i>Opuntia stricta</i> *	Cactaceae	p	North America	3	5.0	0	3	0.1	84/10
<i>Achyranthes aspera</i>	Amaranthaceae	a, p	Mediterranean	2	3.3	2	0	0.1	160/52
<i>Zinnia peruviana</i> *	Asteraceae	a	North to South America	2	3.3	1	1	0.1	45/9
<i>Opuntia ficus-indica</i>	Cactaceae	p	North America	1	1.7	0	1	0.1	139/40
<i>Argemone ochroleuca</i>	Papaveraceae	a	North America	1	1.7	1	0	0.1	96/15
<i>Chenopodium album</i> agg.	Amaranthaceae	a	Eurasia	1	1.7	1	0	0.1	298/28
<i>Datura innoxia</i>	Solanaceae	p, ss	North America	1	1.7	1	0	0.1	126/29
<i>Verbesina encelioides</i>	Asteraceae	a	South America	1	1.7	0	1	0.1	88/12

¹some sources give Eurasia as the region of origin

naturalised in Africa. In particular, *Portulaca oleracea* (56 regions), *Tridax procumbens* (55), *Achyranthes aspera* (52), *Acanthospermum hispidum* (49) and *Gomphrena celosioides* (43) are species that are most widely naturalised in this continent (Table 1).

In terms of distribution of the recorded species by habitats, the majority were concentrated at perennial rivers. Some species, for example, *Alternanthera pungens*, *Gomphrena celosioides* and *Acanthospermum hispidum*, occurred almost exclusively in this habitat, whilst others, for example, *Bidens biternata*, *Malvastrum coromandelianum* and *Parthenium hysterophorus*, were repeatedly recorded also at seasonal rivers and *Opuntia stricta*, *Parthenium hysterophorus* and *Tridax procumbens* on the crests, too (Fig. 3).

The majority of species did not prefer any particular bedrock, with the exception of four species occurring more frequently on granites: *Tridax procumbens* (eight records on granites vs. three on basalts), *Bidens bipinnata*, *Gomphrena celosioides* (four vs. two) and *Opuntia stricta* (three records exclusively on granite). The species occurring more often on basalt bedrock were *Alternanthera pungens* (three vs. five) and *Melanthera scandens* (three vs. one) (Table 1).

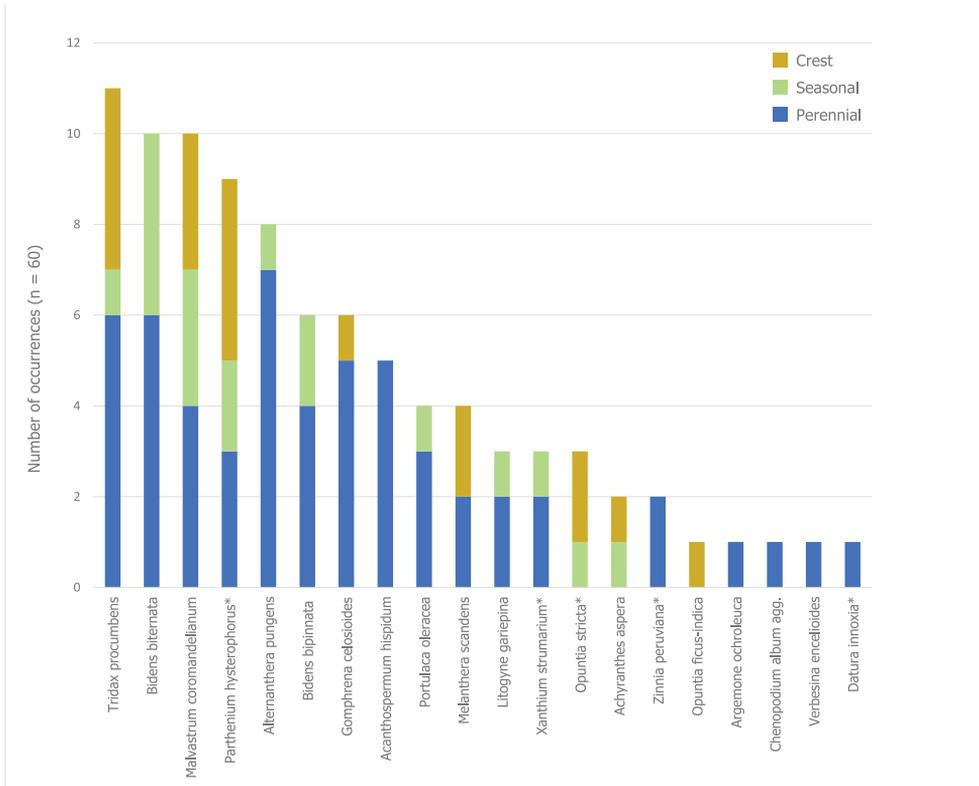


Figure 3. Distribution of alien species in the Kruger National Park according to the savanna habitats delimited within the MOSAIK project (perennial rivers, seasonal rivers, dry crest). Numbers of occurrences (n = 20 per habitat) are shown. Species with * are considered invasive in KNP.

Levels of invasion in savanna habitats: rivers and beyond

The average number of alien species per plot was relatively low, 1.6 ± 1.7 (mean \pm S.D.), but only 21 plots out of 60 were alien free, meaning that 65% of plots harboured some alien species. The maximum number of alien species per plot was seven. On average, the alien species made up 2.2% (range 0–11.9%) of all species in a plot. The numbers of alien and native species in plots were not correlated ($r = 0.067$, $DF_{resid} = 58$, $p = 0.609$).

Testing the average number of aliens per plot (Fig. 4A) revealed a significant effect of habitat (LMM: deletion test, $DF_{model} = 5$ vs. 7, L-ratio = 22.175, $p < 0.001$), with perennial rivers being significantly richer than seasonal rivers and crests (LMM: $DF_{error} = 36$, $T = -2.751$, $p = 0.0092$; $DF_{error} = 36$, $T = -3.662$, $p = 0.0008$, respectively).

In total, there were 17, 11 and 8 species recorded at perennial rivers, seasonal rivers and on the crest, respectively, and the total numbers of alien species in a habitat (Fig. 4B) significantly differed (log-linear model: deletion test, $DF_{resid} = 2$ vs. 4, Dev. = -10.76, $p = 0.005$). Perennial rivers had significantly more aliens than crests ($z = -2.842$, $p = 0.0125$).

and seasonal rivers ($z = 2.361$, $p = 0.048$). Only three species (*Tridax procumbens*, *Malvastrum coromandelianum* and *Parthenium hysterophorus*) occurred in all three habitats. Perennial rivers had six species occurring exclusively in this habitat and another six they share with seasonal rivers (see Fig. 3), one species was found exclusively on crests (*Opuntia ficus-indica*) and none only at seasonal-river sites (Fig. 5). In terms of the number of occurrences (defined as the sum of the numbers of records over all alien species), the importance of the perennial rivers was even more pronounced. The 55 occurrences at perennial rivers

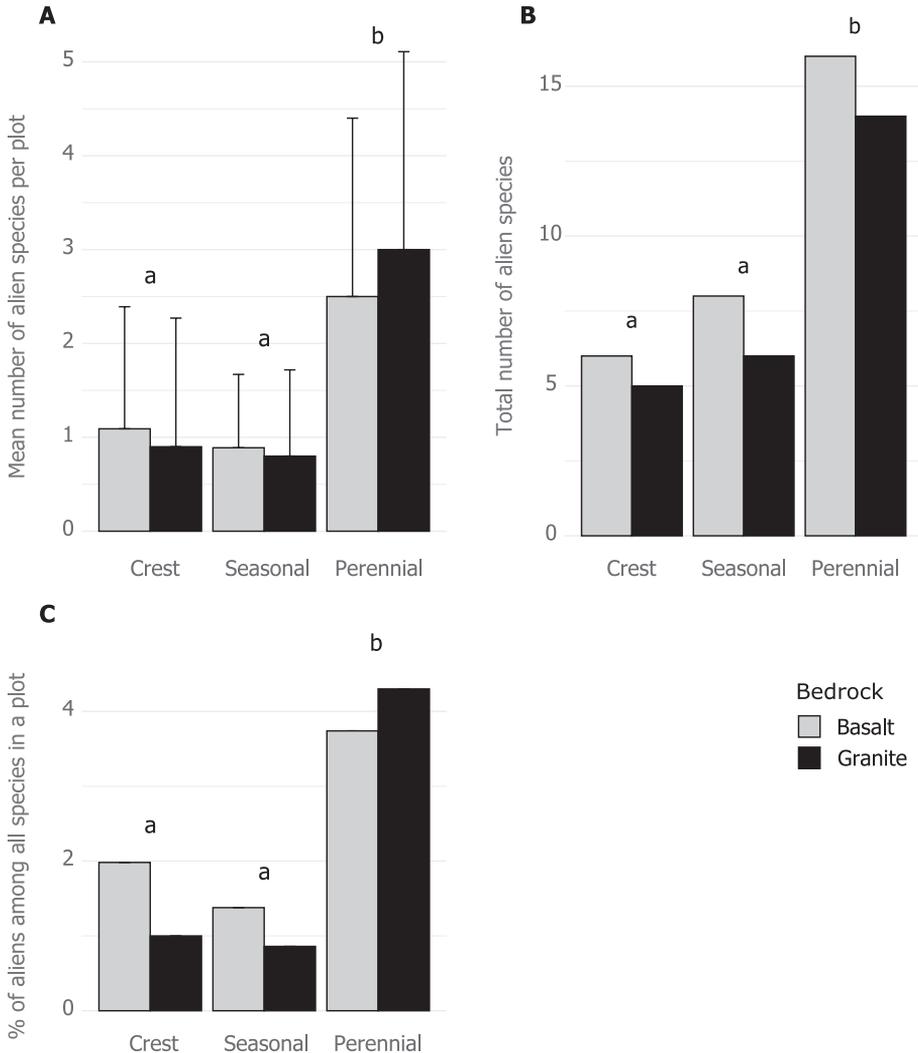


Figure 4. Level of invasion by bedrock and habitat. **A** Mean numbers \pm S. D. of species per plot ($n = 20$ per habitat) **B** total species numbers and **C** percentage of alien species amongst all species in a plot are shown for particular factors. The habitats bearing the same letter were not significantly different in the respective characteristics; the effect of bedrock was not significant.

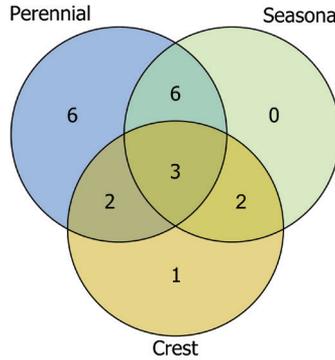


Figure 5. Venn diagram showing the sharing of alien species by habitats in the Kruger National Park. *Tridax procumbens*, *Malvastrum coromandelianum* and *Parthenium hysterophorus* were the species recorded at all three habitats.

(compared to 18 at seasonal rivers and 18 in crest plots) means that 60.4% of all alien species' occurrences were associated with the former habitat.

The percentage of alien species per plot (Fig. 4C) differed amongst habitats (LMM: deletion test, $DF_{\text{model}} = 5$ vs. 7, L-ratio = 7.884, $p = 0.005$), with perennial rivers being marginally significantly richer than crests (LMM: $DF_{\text{error}} = 36$, $T = -2.004$, $p = 0.053$) and significantly richer than seasonal rivers (LMM: $DF_{\text{error}} = 36$, $T = -2.218$, $p = 0.033$).

Levels of invasion: no effect of bedrock

Of the 20 alien species recorded in total, 16 were found on granites and 17 on basalts, with corresponding averages per plot 1.6 ± 1.9 and 1.5 ± 1.5 , respectively. Neither the main effect of bedrock, nor the bedrock \times habitat interaction had significant effects on the mean number of aliens per plot (LMM: deletion test, $DF_{\text{model}} = 6$ vs. 7, L-ratio = 0.895, $p = 0.344$, and $DF_{\text{model}} = 7$ vs. 9, L-ratio = 0.294, $p = 0.634$, respectively; Fig. 4A), the total number of aliens in a given category (log-linear model: deletion test, $DF_{\text{resid}} = 2$ vs. 3, Dev. = -4.55, $p = 0.5$; and $DF_{\text{resid}} = 0$ vs. 2, Dev. = -0.056, $p = 0.972$, respectively; Fig. 4B) and the percentage of aliens amongst all species per plot (LMM: deletion test, $DF_{\text{resid}} = 6$ vs. 7, L-ratio = 1.242, $p = 0.537$; and $DF_{\text{resid}} = 5$ vs. 7, L-ratio = 1.355, $p = 0.322$, respectively; Fig. 4C).

Discussion

It has been suggested that the negative impacts of plant invasions in protected areas in African savannas are less dramatic than in the savanna regions and ecosystems in the Neotropics and Australia. Foxcroft et al. (2010) reviewed this issue and concluded that

the rather low levels of savanna invasions are in part due to lower rates of intentional plant introductions to Africa, for example, less widespread planting of large numbers of grass species, the key role of large mammalian herbivores in these ecosystems, historical and biogeographical issues related to the regions of origin of introduced species and the adaptation of African ecosystems to fire. Most of these factors are especially relevant in large protected areas, such as KNP, where the above constraints to invasion are strengthened by the fact that the protected areas act as barriers to colonisation of alien species from the outside (Pyšek et al. 2003; Foxcroft et al. 2011). They also act as refuges protecting native species against combined effects of invasion and climate change, as shown for European protected areas (Gallardo et al. 2017).

Due to research conducted mostly in the temperate areas, rivers have long been recognised as major pathways of alien plant introduction to new regions; they are highly prone to invasion by alien plants, largely because of their dynamic hydrology that makes them conduits for efficient dispersal of propagules (Planty-Tabacchi et al. 1996; Hood and Naiman 2000; Sibiya 2019). Fluctuating water levels provide space for new species by removing vegetation and increasing resources by making nutrients and light available (Richardson et al. 2007; Sibiya 2019). As most rivers flow through human settlements, there are multiple opportunities for the introduction of alien propagules into riparian zones and there is quantitative evidence that alien plants concentrate in riparian sites (e.g. Chytrý et al. 2008; Pyšek et al. 2010). While some species invading riparian habitats remain restricted to the vicinity of the river, other plants spread away from the river often after a considerable time lag spanning decades (Čuda et al. 2020). This represents a major threat to vegetation beyond the riparian ecosystems and can start new invasions into habitats previously not affected.

However, we found that the threat of invasion beyond the main perennial rivers and adjacent floodplain areas, where the major invaders are concentrated (Jarošík et al. 2011), is currently relatively minor in KNP. The majority of aliens recorded by our survey still occur at plots located near perennial rivers – but not all (Fig. 1). Some of the species not confined to rivers are amongst the most widespread, for example, *Bidens biternata*, *Malvastrum coromandelianum* and *Parthenium hysterophorus* and were repeatedly recorded also at seasonal-river plots. More importantly, two of the most invasive plants in the park, *Opuntia stricta* and *Parthenium hysterophorus*, were also found on the crest plots. Apparently, despite the successful biological control of *Opuntia stricta* in KNP in 1980s–1990s (Foxcroft et al. 2004), this invasive species is still present in dry areas of the savanna and could potentially start a new invasion. In addition, almost all of the alien plants we recorded in KNP have successfully naturalised in many regions of the world, half of them in more than 100 regions, which needs to be taken as a warning of the potential for many species to become serious invaders in KNP in the future. That these alien species successfully persist in subtropical and tropical climates is evident from all of them having naturalised in many other African regions, too, and five being distributed in more than 40 regions on this continent (*Portulaca oleracea*, *Tridax procumbens*, *Achyranthes aspera*, *Acanthospermum hispidum* and *Gomphrena celosioides*). None of these most widely naturalised species in

Africa is currently considered invasive in KNP, but attention should be paid by park management, especially in surveillance programmes.

It needs to be pointed out, however, that alien species recorded in our plots mostly occur in low abundance. *Bidens bipinnata* occasionally reached up to 15% of cover and *Alternanthera pungens* and *Acanthospermum hispidum* ~5%. Aliens also account for a rather small proportion of the total plant richness; on average, there were less than two alien species per plot, with maximum of seven and contribute less than 3% to the total plot richness. However, in two plots at perennial rivers, alien species contributed 11.9% and 9.2% and additional seven plots harboured more than 5% of aliens. This, together with the fact that almost three quarters of all sampled plots had at least one alien species, indicates that KNP needs to monitor the occurrence of these species, ideally on a regular and systematic basis. Our detailed survey covered, in cumulative terms, 15 hectares and, extrapolating the figures to the total park area, implies that alien plant species are already a fairly common phenomenon throughout the whole park.

Acknowledgements

The study was supported by grant no. 18-18495S (Czech Science Foundation), EXPRO grant no. 19-28807X (Czech Science Foundation), long-term research development project RVO 67985939 (Czech Academy of Sciences) and projects UNCE204069 and PRIMUS/17/SCI/8 (Charles University). The project was registered as PYSK1432 with SANParks. LCF thanks SANParks and acknowledges support from the DSI-NRF Centre for Invasion Biology, Stellenbosch University. Thanks are to our guards Obert Mathebula, Thomas Rikombe, Desmond Mabaso, Herman Ntimane, Annoit Mashele, Isaac Sedibe, Priska Rikombe and Velly Ndlovu for keeping us safe in the field. We thank Elizabete Marchante, Nina Šajna and Sven Jelaska for helpful comments on the manuscript.

References

- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Carruthers J (1995) *The Kruger National Park: A Social and Political History*. University of Natal Press, Natal, 170 pp.
- Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology* 45: 448–458. <https://doi.org/10.1111/j.1365-2664.2007.01398.x>

- Crawley MJ (2007) *The R Book*. JohnWiley & Sons, Chichester, 950 pp. <https://doi.org/10.1002/9780470515075>
- Čuda J, Skálová H, Pyšek P (2020) Spread of *Impatiens glandulifera* from riparian habitats to forests and its associated impacts: Insights from a new invasion. *Weed Research* 60: 8–15. <https://doi.org/10.1111/wre.12400>
- De Poorter M (2007) Invasive alien species and protected areas: A scoping report. Part 1. Scoping the scale and nature of invasive alien species threats to protected areas, impediments to IAS management and means to address those impediments. Global Invasive Species Program, Invasive Species Specialist Group. http://www.issg.org/gisp_publications_reports.htm
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M [Eds] (1989) *Biological Invasions: A Global Perspective*. John Wiley & Sons, Chichester, 525 pp.
- du Toit JT, Biggs H, Rogers KH [Eds] (2003) *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*. Island Press, Washington DC, 492 pp.
- Essl F, Bacher S, Genovesi P, Hulme PE, Jeschke JM, Katsanevakis S, Kowarik I, Kühn I, Pyšek P, Rabitsch W, Schindler S, van Kleunen M, Vilà M, Wilson JRU, Richardson DM (2018) Which taxa are alien? Criteria, applications, and uncertainties. *BioScience* 68: 496–509. <https://doi.org/10.1093/biosci/biy057>
- Foxcroft LC, Jarošík V, Pyšek P, Richardson DM, Rouget M (2011) Protected-area boundaries as filters of plant invasions. *Conservation Biology* 25: 400–405. <https://doi.org/10.1111/j.1523-1739.2010.01617.x>
- Foxcroft LC, Pyšek P, Richardson DM, Genovesi P [Eds] (2013) *Plant Invasions in Protected Areas: Patterns, Problems and Challenges*. Springer, Dordrecht, 656 pp. <https://doi.org/10.1007/978-94-007-7750-7>
- Foxcroft LC, Pyšek P, Richardson DM, Genovesi P, MacFadyen S (2017) Plant invasion science in protected areas: Progress and priorities. *Biological Invasions* 19: 1353–1378. <https://doi.org/10.1007/s10530-016-1367-z>
- Foxcroft LC, Richardson DM, Rejmánek M, Pyšek P (2010) Alien plant invasions in tropical and sub-tropical savannas: Patterns, processes and prospects. *Biological Invasions* 12: 3913–3933. <https://doi.org/10.1007/s10530-010-9823-7>
- Foxcroft LC, Richardson DM, Rouget M, MacFadyen S (2009) Patterns of alien plant distribution at multiple spatial scales in a large national park: Implications for ecology, management and monitoring. *Diversity and Distributions* 15: 367–378. <https://doi.org/10.1111/j.1472-4642.2008.00544.x>
- Foxcroft LC, Richardson DM, Wilson JRU (2008) Ornamental plants as invasive aliens: Problems and solutions in Kruger National Park, South Africa. *Environmental Management* 41: 32–51. <https://doi.org/10.1007/s00267-007-9027-9>
- Foxcroft LC, Rouget M, Richardson DM, MacFadyen S (2004) Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: Environmental determinants and propagule pressure. *Diversity and Distributions* 10: 427–437. <https://doi.org/10.1111/j.1366-9516.2004.00117.x>
- Foxcroft LC, Spear D, van Wilgen NJ, McGeoch MA (2019) Assessing the association between pathways of alien plant invaders and their impacts in protected areas. *NeoBiota* 43: 1–25. <https://doi.org/10.3897/neobiota.43.29644>

- Gallardo B, Aldridge DC, González-Moreno P, Pergl J, Pizarro M, Pyšek P, Thuiller W, Yesson C, Vilà M (2017) Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology* 23: 5331–5343. <https://doi.org/10.1111/gcb.13798>
- Hood WG, Naiman RJ (2000) Vulnerability of riparian zones to invasion by exotic vascular plants. *Plant Ecology* 148: 105–114. <https://doi.org/10.1023/A:1009800327334>
- Hui C, Foxcroft LC, Richardson DM, MacFadyen S (2011) Defining optimal sampling effort for large-scale monitoring of invasive alien plants: A Bayesian method for estimating abundance and distribution. *Journal of Applied Ecology* 48: 768–776. <https://doi.org/10.1111/j.1365-2664.2011.01974.x>
- Hulme PE, Pyšek P, Pergl J, Jarošík V, Schaffner U, Vilà M (2014) Greater focus needed on alien plant impacts in protected areas. *Conservation Letters* 7: 459–466. <https://doi.org/10.1111/conl.12061>
- Jarošík V, Pyšek P, Foxcroft LC, Richardson DM, Rouget M, MacFadyen S (2011) Predicting incursion of plant invaders into Kruger National Park, South Africa: The interplay of general drivers and species-specific factors. *PLoS ONE* 6: e28711. <https://doi.org/10.1371/journal.pone.0028711>
- MacFadyen S, Hui C, Verburg PH, Van Teeffelen AJA (2016) Quantifying spatiotemporal drivers of environmental heterogeneity in Kruger National Park, South Africa. *Landscape Ecology* 31: 2013–2029. <https://doi.org/10.1007/s10980-016-0378-6>
- MacFadyen S, Zambatis N, Van Teeffelen AJA, Hui C (2018) Long-term rainfall regression surfaces for the Kruger National Park, South Africa: A spatio-temporal review of patterns from 1981–2015. *International Journal of Climatology* 38: 2506–2519. <https://doi.org/10.1002/joc.5394>
- Moodley D, Foxcroft LC, Novoa A, Pergl J, Pyšková K, Pyšek P (2020) Invasive alien species add to the uncertain future of protected areas. *NeoBiota* 57: 1–5. <https://doi.org/10.3897/neobiota.57.52188>
- Mueller-Dombois D, Ellenberg H (1974) *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York, 547 pp.
- Planty-Tabacchi AM, Tabacchi E, Naiman RJ, Deferrari C, Décamps H (1996) Invasibility of species rich communities in riparian zones. *Conservation Biology* 10: 598–607. <https://doi.org/10.1046/j.1523-1739.1996.10020598.x>
- Pyšek P, Bacher S, Chytrý M, Jarošík V, Wild J, Celesti-Grappo L, Gassó N, Kenis M, Lambdon PW, Nentwig W, Pergl J, Roques A, Sádlo J, Solarz W, Vilà M, Hulme PE (2010) Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and Biogeography* 19: 317–331. <https://doi.org/10.1111/j.1466-8238.2009.00514.x>
- Pyšek P, Genovesi P, Pergl J, Monaco A, Wild J (2013) Invasion of protected areas in Europe: An old continent facing new problems. In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) *Plant Invasions in Protected Areas: Patterns, Problems and Challenges*. Springer, Dordrecht, 209–240. https://doi.org/10.1007/978-94-007-7750-7_11
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ,

- Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* (in press). <https://doi.org/10.1111/brv.12627>
- Pyšek P, Jarošík V, Kučera T (2003) Inclusion of native and alien species in temperate nature reserves: An historical study from Central Europe. *Conservation Biology* 17: 1414–1424. <https://doi.org/10.1046/j.1523-1739.2003.02248.x>
- Pyšek P, Pergl J, Essl F, Lenzner B, Dawson W, Kreft H, Weigelt P, Winter M, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Dullinger S, Ebel AL, Figueiredo E, Fuentes N, Genovesi P, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Maurel N, Meerman J, Morozova O, Moser D, Nickrent D, Nowak PM, Pagad S, Patzelt A, Pelsers PB, Seebens H, Shu W, Thomas J, Velasco M, Weber E, Wieringa JJ, Baptiste MP, van Kleunen M (2017) Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia* 89: 203–274. <https://doi.org/10.23855/preslia.2017.203>
- Pyšek P, Richardson DM, Rejmánek M, Webster G, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143. <https://doi.org/10.2307/4135498>
- R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ (2007) Riparian vegetation: Degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions* 13: 126–139. <https://doi.org/10.1111/j.1366-9516.2006.00314.x>
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6: 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Shackleton RT, Foxcroft LC, Pyšek P, Wood LE, Richardson DM (2020) Assessing biological invasions in protected areas after 30 years: Revisiting nature reserves targeted by the 1980s SCOPE programme. *Biological Conservation* 243: 108424. <https://doi.org/10.1016/j.biocon.2020.108424>
- Sibiya TE (2019) Riparian plant community change and alien plant invasions following geomorphological change in the Sabie River, Kruger National Park, South Africa. MSc Thesis, Stellenbosch University, Stellenbosch.
- Spear D, Foxcroft LC, Bezuidenhout H, McGeoch MA (2013) Human population density explains alien species richness in protected areas. *Biological Conservation* 159: 137–147. <https://doi.org/10.1016/j.biocon.2012.11.022>
- van der Maarel E (1979) Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 38: 97–114. <https://doi.org/10.1007/BF00052021>
- van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL,

- Patzelt A, Pelsers PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu W, Thomas J, Velasco M, Wieringa JJ, Pyšek P (2015) Global exchange and accumulation of non-native plants. *Nature* 525: 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen M, Pyšek P, Dawson W, Essl F, Kreft H, Pergl J, Weigelt P, Stein A, Dullinger S, König C, Lenzner B, Maurel N, Moser D, Seebens H, Kartesz J, Nishino M, Aleksanyan A, Ansong M, Antonova LA, Barcelona JF, Breckle SW, Brundu G, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Conn B, de Sá Dechoum M, Dufour-Dror J-M, Ebel A-L, Figueiredo E, Fragman-Sapir O, Fuentes N, Groom QJ, Henderson L, Inderjit, Jogan N, Krestov P, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Nickrent D, Nowak A, Patzelt A, Pelsers PB, Shu W-S, Thomas J, Uludag A, Velasco M, Verkhosina A, Villaseñor JL, Weber E, Wieringa J, Yazlık A, Zeddam A, Zykova E, Winter M (2019) The Global Naturalized Alien Flora (GloNAF) database. *Ecology* 100: e02542. <https://doi.org/10.1002/ecy.2542>
- van Wilgen BW, Fill JM, Govender N, Foxcroft LC (2017) An assessment of the evolution, costs and effectiveness of alien plant control operations in Kruger National Park, South Africa. *NeoBiota* 35: 35–59. <https://doi.org/10.3897/neobiota.35.12391>
- Venter FJ (1990) A classification of land for management planning in the Kruger National Park. PhD Thesis, University of South Africa, Pretoria.