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Patterns of alien plant distribution in a river landscape following an extreme flood

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Abstract

The availability of suitable patches and gaps in the landscape is a crucial determinant of invasibility for alien plants. The type and arrangement of patches in the landscape may both facilitate and obstruct alien plant invasions, depending on whether alien species perceive the patches as barriers. In February 2000 tropical weather systems caused an extreme flood with an estimated return interval of 90 to 200 years in the Sabie River, South Africa. The impact of the 2000 flood on the Sabie River landscape provides an array of patches that may provide suitable resources for the establishment of alien plants. This study examines the distribution of alien plants in relation to patchiness of the Sabie River landscape. Our hypothesis was that if certain patches in the river landscape do not represent environmental barriers to alien plant invasion, alien species will occur preferentially in these patch types. The Sabie River within Kruger National Park [KNP] was divided into six patch types (zones, channel types, elevations, geomorphic units, substrates and flood imprint types). We then examined the distribution of native and alien woody and herbaceous density and species richness in patches. The density and species richness of alien plants in the Sabie River in KNP is very low when compared to the density and species richness of native plants. Some patches (bedrock distributary and braid bar geomorphic units) contained higher density and richness of alien plants compared to the other patches examined, indicating that these locations in the river landscape offer the resources necessary for alien plant establishment. Individual alien species are also associated with different parts of the river landscape. Failure of large numbers of alien plants to establish after the 2000 flood is most likely due to a combination of factors—the plant specific barriers imposed by landscape patchiness, the high abundance and richness of native vegetation leading to competition, and for some species certainly, the clearing by the management (Working for Water) programme.

Keywords: Biological invasions; Disturbance; Geomorphology; Kruger National Park; Riparian ecosystems; River landscape heterogeneity

1. Introduction

The availability of suitable patches and gaps in the landscape is an important determinant of the susceptibility of riparian ecosystems to alien plant invasions (Richardson et al., 2007). Patches may occur as inherent variability caused by climate, topography and geology (White and Harrod, 1997), or may be generated via the reorganization of landscapes by abiotic disturbances such as fires, floods, hurricanes, and anthropogenic land-surface alterations (Pickett and White, 1985). Patches may also be created by biotic disturbances such as disease outbreaks and successional change (Knight, 1987; Pacala and Crawley, 1992). Thus, patches of early successional communities, open space, and resource-rich patches often owe their existence to disturbance events (Pickett, 1998). Numerous studies have examined the response of invasive species to disturbance and disturbance-generated patches in the landscape (for example: Hobbs, 1989; Mack and D'Antonio, 1998; Hobbs

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and Heunneke, 1992; Holmes et al., 2000; Berlow et al., 2001; Brooks and Pyke, 2001; Grace et al., 2001; Cannas et al., 2002; Leishman et al., 2004). However, not all gaps and patches in a landscape are invaded by alien species. Rather, to successfully invade and ultimately transform ecosystems, alien plant species must overcome a series of geographic, environmental, reproductive and dispersal barriers (Richardson et al., 2000), which are arrayed spatially within the landscape (Fig. 1). Although numerous studies have investigated the role of resource availability (e.g. Hobbs and Heunneke, 1992), and the fluctuating availability of those resources (Davis et al., 2000), disturbance regimes (e.g. Hobbs, 1989; Brooks and Pyke, 2001; Grace et al., 2001), and empty niches (e.g. Cannas et al., 2002) in facilitating invasions, we know of only a few studies that have explicitly examined the role of landscape patches in the context of invasibility (With, 2002, 2004). The type and arrangement of patches in the landscape may both facilitate and obstruct alien plant invasions, depending on whether an alien plant taxon perceives patches as a barrier, or as an area of suitable resource availability.

Rivers are important conduits for alien plant invasions (Pyšek and Prach, 1994; Foxcroft et al., 2007; Richardson et al., 2007), because rivers are continuous, highly connected components of the landscape. This connectivity facilitates the movement of native organisms between isolated areas in the landscape (Van Wilgen et al., 2007), but also provides corridors for the transport of unwanted alien organisms (Foxcroft et al., 2007). Riparian areas are particularly prone to alien plant invasions because of their dynamic hydrology, the provision of favourable resource, moisture and nutrient conditions, and frequent disturbance by floods (Tickner et al., 2001). In South Africa's Kruger National Park [KNP] many invasive plant species have spread from areas

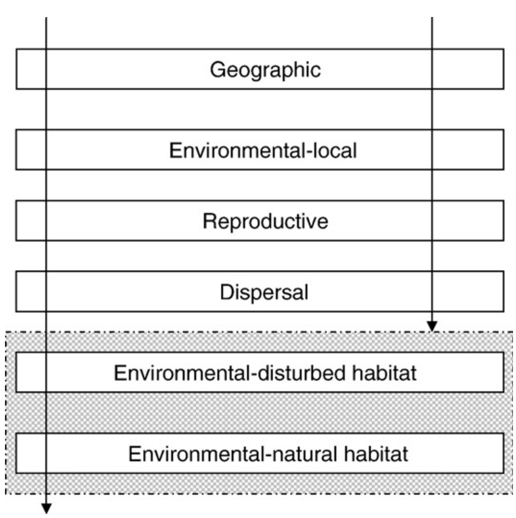

Fig. 1. Conceptual barriers in the invasion process (from Richardson et al., 2000). In the case of the Sabie River, alien plants will have overcome the first four barriers through various means, but need to overcome the local environmental barriers to become invasive. As disturbance is a natural feature of riparian systems, we see these barriers as being integrated. The reorganisation of the river landscape after a large flood event creates barriers to various alien plants, through the reorganisation of habitats, and the extent to which a particular alien plant perceives the patch as a barrier to, or a gap for, invasion.

outside the park to areas inside the park along river corridors (Foxcroft and Richardson, 2003; Foxcroft et al., 2007). Given the multiple land uses and the abundance and diversity of invasive alien plant species in the watersheds drained by the major rivers of the KNP (Foxcroft et al., 2007; Beater et al., 2008-this issue; Witkowski and Garner, 2008-this issue), the incursion of alien species along river corridors is a major threat to riparian zones of KNP and, in turn, to the objectives of the park to maintain biodiversity (KNP, 2006).

Disturbance is a fundamental driver of patchiness in river landscapes. The hydrological (flow regime) and hydraulic actions of water are primary agents of disturbance, creating an irregular, dynamic and shifting mosaic of biotic and abiotic patches at multiple spatial and temporal scales within the river landscape (Tabacchi et al., 1998; Malard et al., 2000; Arscott et al., 2002; Dixon, 2003). In the Sabie River, which flows through KNP, a hierarchy of geomorphological river system organization has been derived (Van Niekerk et al., 1995). The catchment, zone, macro-reach, channel type, reach, geomorphic unit and micro-site divisions of the hierarchy can be viewed as patches in the river landscape (Rogers and O'Keefe, 2003). The type and arrangement of these patches subsequently influences the distribution of riparian vegetation assemblages because each level provides a characteristic physical environment (Van Coller et al., 2000). However, these patches are not static in space and time and patches may be formed and reformed by flow events of various magnitude and duration (Rountree et al., 2000; Rountree and Rogers, 2004).

In February 2000, tropical weather systems caused an extreme flood with an estimated return interval of 90 to 200 years in the Sabie River (Smithers et al., 2001). Flow peaked at an estimated 3000 m^3/s where the river enters KNP and at 7000 m^3/s where the river exits the park 100 km downstream at the border with Mozambique (Heritage et al., 2001). These discharges compare with typical wet-season (November–March) base flows of 15–20 m^3/s and dry season base flows of 3–5 m^3/s. The flood markedly altered the spatial pattern of channel type, geomorphic unit and micro-site patches in the river landscape by eroding and depositing sediment, and removing large amounts of riparian vegetation (Parsons et al., 2006). The flood also triggered substantial recruitment of riparian plants (Parsons et al., 2005), including alien species. As would be expected following disturbance events, the imprint left on the Sabie River landscape by the 2000 flood provides a range of patch types that potentially provide suitable resources for the establishment of alien plants. However, the type and arrangement of patches in the Sabie River landscape could also represent barriers to establishment. Although rivers are effective corridors of alien plant invasion and floods are effective dispersers of propagules, we do not know how alien plants overcome environmental barriers present in river landscapes after disturbance, in order to become established. Therefore, in developing an understanding of the role of barriers in the invasion process, this study examines the distribution of alien plants in relation to patchiness of the Sabie River landscape following the 2000 flood. We know that the flood water volume was many orders of magnitude higher than average flows, and that the flood reset the river landscape to an early stage of the invasion process. There is also a substantial source of propagules in the upper catchment of the river (Foxcroft et al., 2007) and during the flood we assume these propagules would be transported down the river. Our hypothesis is that, assuming propagules have dispersed and are available (Fig. 1), if certain patches in the river landscape do not represent an environmental barrier to alien plant invasion, alien species will have preferences for these patch types. Conversely, if patches in the river landscape do represent an environmental barrier, alien species will not be present in high density and richness in these patch types.

2. Materials and methods

2.1. Study area

The Sabie River rises in the Mpumalanga Highlands at an altitude of 2200 m and flows eastward for 210 km across the Lowveld and Lebombo geomorphological zones until its confluence with the Incomati River in Mozambique at an altitude of 150 m. It has a catchment area of 7096 km^2, almost half (48%) of which occurs inside KNP, where land is predominantly managed for conservation. Land uses in the portion of the catchment outside KNP comprise 20% cultivated lands, 7% degraded lands, 50% natural vegetation and 20% pine (*Pinus* spp.) and eucalypt (*Eucalyptus* spp.) forest plantations (Foxcroft et al., 2007; Beater et al., 2008-this issue) and other uses, including human settlements and towns, 3%. Due to the high invasive species abundance and richness in the portion of watersheds outside KNP (Beater et al., 2008-this issue), efforts have been made to assess risk of invasion down the rivers into KNP (Foxcroft et al., 2007). Management projects are currently underway in KNP to address the invasion of alien plant species by a number of vectors. The largest programme currently in operation aims at continuous follow-up or maintenance control operations against a suite of invasive riparian plant species by the national Working for Water program (Foxcroft and Richardson, 2003; Freitag-Ronaldson and Foxcroft, 2003; Morris et al., 2008-this issue). This largely entails the use of mechanical and chemical methods to control woody shrubs, and uproot annual herbaceous weeds (see Morris et al., 2008-this issue for further details on the clearing programme). All areas on both sides of the Sabie River are searched, where accessible, and all alien plants are removed. The most commonly controlled woody alien plants include *Chromolaena odorata*, *Lantana camara*, *Melia azedarach*, *Nicotiana glauca*, *Ricinus communis*, *Senna didymobotrya*, while the most widespread herbaceous alien plants include *Argemone* spp., *Datura* spp. and *Xanthium* spp. Ideally, the areas controlled should be added to this analysis in order to evaluate the influence that management has had on alien plant distribution. Unfortunately, although GIS data of the control areas are available, these readings were not sufficiently accurate to be compatible with the very precise nature of the data collected for the present study. Therefore, we are not certain whether the alien plants occur where they are because they were not cleared from those patches, or, because those patches allow higher rates of establishment due to the characteristics of the patch itself. However, the entire area should have been equally searched during control operations and should not bias our results.

Table 1
Description of patch types in the Sabie River landscape

Patch type	Description
Zone	Identified from maps
Upper	Granite geology, 3000 m^3s^{-1} flood discharge
Mid	Granite geology, intermediate discharge
Lower	Basalt geology, 7000 m^3s^{-1} flood discharge
Geomorphological channel type	Identified from aerial photographs (see Parsons et al., 2006)
Braided	Braiding within the confined channel
Pool rapid	Pools separated by bedrock rapids
Bedrock anastomosing	The connection of separate parts of a branching system to form a network; multiple channels flowing through bedrock
Mixed anastomosing	Multiple channels flowing through alluvium on a bedrock base
Elevation	Identified using a high resolution digital elevation model derived from LIDAR data
0–1 m, 1–2 m, up to >9 m	Elevation is the vertical profile, from the level of the water, at 1 m intervals
Geomorphic unit	Identified from aerial photographs
Bedrock core bar	Accumulation of finer consolidated sediments and sands on top of bedrock in bedrock anastomosing areas
Bedrock distributary	An individual active channel in a bedrock anastomosing system containing no consolidated and/or unconsolidated sediment
Bedrock pavement	Bedrock bed or base
Braid bar	Accumulation of unconsolidated sediment attached to the side of the channel, possibly associated with a rip-channel causing flow to diverge over a scale that approximates to the channel width
Lateral bar	Accumulation of unconsolidated sediment attached to the side of the channel, possibly associated with a rip-channel at the base of the macro-channel, forming in areas of reduced energy flow
Macro-channel bank	The main/edge bank of the macro-channel which extends across the incised valley and contains the sedimentary deposits and riparian vegetation
Substrate	Measured in the field as the substrate in which each plant is rooted. Percent substrate composition in each plot was then calculated.
Bedrock	Bedrock bed / base / boulder
Fines	Silt, clay and organic particles, <0.06 mm
Sand	Coarse river sand, 0.06–2 mm
Sand and fines	Mixed sand and fine substrate
Bedrock and fines	Mixed bedrock and fine substrate
Bedrock and sand	Mixed bedrock and sand substrate
Flood imprint	Identified using a GIS (see Parsons et al., 2005 and 2006)
Vegetated to physical	Areas that were vegetated by reeds, shrubs, trees or herbaceous vegetation prior to the 2000 flood, but are now areas of physical rock, sand or water states following the flood.
Stayed vegetated	Areas that were vegetated by reeds, shrubs, trees or herbaceous vegetation prior to the 2000 flood, and remain as one of these vegetated states following the flood
Stayed physical	Areas that were a physical rock, sand or water state prior to the 2000 flood, and remain as one of these physical states following the flood
Vegetated or physical to debris	Areas vegetated by reeds, shrubs, trees or herbaceous vegetation, or that were a physical rock, sand or water state prior to the 2000 flood, but are now areas of woody debris following the flood

This study focused on the distribution of alien plants within KNP, along the 110 km main-stem section of the Sabie River. The Sabie River has a geomorphologically complex, mixed bedrock and alluvial landscape, where one or more active channels flow within an incised macro-channel that ranges in width from 250–800 m and 8–15 m in depth (Van Niekerk et al., 1995). Macro reach, channel type, geomorphic unit and micro-site are the nested levels of landscape organization relevant to the section of river within KNP (Van Niekerk et al., 1995). Micro-sites are defined by their sediment character and elevation, in relation to the geomorphic unit in which they occur. Geomorphic units such as bedrock core bars, distributary channels, lateral bars, pools, riffles, mid-channel bars and benches occur together in specific combinations and proportions to characterise a channel type. Four dominant channel types have been identified in the Sabie River: braided (braiding within the confines of the macro-channel), pool rapid (pools separated by bedrock rapids), mixed anastomosing (multiple channels flowing through alluvium on a bedrock base) and bedrock anastomosing (multiple channels flowing through bedrock fissures) (Van Niekerk et al., 1995). Macro-reaches, or zones, are characterized by broad changes in geology and discharge capacity in a downstream direction.

The Sabie River exhibits a seasonal, perennial flow regime but is subject to discharge extremes characteristic of semi-arid areas (Parsons et al., 2006). Inundation and disturbance of the river landscape by river flows is related to lateral and vertical topography of the template. The macro-channel is divided into two areas, namely the higher elevation macro-channel bank and the lower elevation macro-channel floor. The macro-channel floor can be divided into flow inundation areas, in which elevation is related to the frequency of inundation (Heritage et al., 1999). The active area is inundated annually for prolonged periods during both wet and dry seasons, or intermittently for short periods by small floods during the wet season (Parsons et al., 2006). The ephemeral area is only inundated during extreme floods.

2.2. Data collection and analysis

The Sabie River landscape was divided into six patch types based on physical and environmental characteristics (Table 1). Zones represent the broad change in geology and discharge capacity in a downstream direction. Channel types represent differences in macro-channel width, channel gradient and geomorphic unit composition (Van Niekerk et al., 1995). Elevation represents differential space–time inundation of the physical

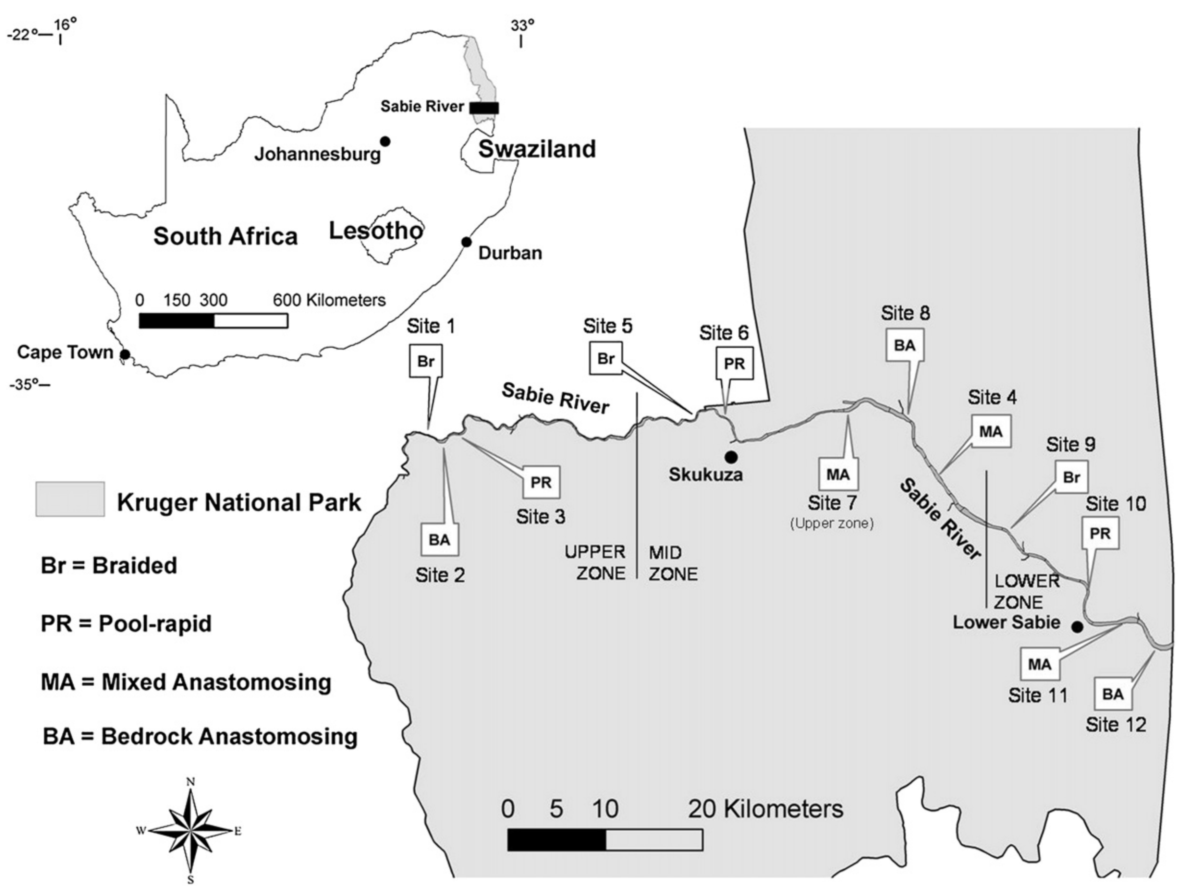

Fig. 2. Location of sampling sites within zones and geomorphological channel types along the Sabie River. The inset places the study site in context with the rest of South Africa.

template by flows of different magnitudes. Geomorphic units represent differences in the bedform morphology of the channel, where different geomorphic units occur at different elevations and have different substrate character (Heritage and Moon, 2000). Substrate represents the texture of the underlying sediment. Flood imprints represent the physical change in the river landscape due to the 2000 flood, and are calculated on the basis of whether an area of the river landscape changed state, or remained as the same state, following the 2000 flood (Parsons et al., 2005). Thus, each of the six patch types has characteristic environmental conditions that may pose an environmental barrier to the establishment of alien plants.

Twelve sampling sites were stratified across zones and channel types (Fig. 2). Woody riparian vegetation was sampled at each site between July and October 2004, in 30 × 5 m plots running contiguously along transects placed across the river (perpendicularly) between the tops of the macro-channel banks. Herbaceous riparian vegetation was sampled at each site between April and July 2005 in 5 × 5 m plots placed at 20 m intervals along the centre of the woody vegetation transect. Real time differential GPS and a GIS were used to mark accurate plot boundaries. In each plot we identified and counted native and alien plants. Species nomenclature follows Germishuizen and Meyer (2003). The abundance of each species in each plot was converted to density (number of plants per ha), and species richness was calculated as the number of species in each plot. There are 548 plots in the woody vegetation data set and 156 plots in the herbaceous vegetation data set.

To determine the density and species richness of native and alien woody and herbaceous vegetation in the six patches, plots were assigned to each of the categories listed in Table 1. Each plot fell within a certain zone, geomorphological channel type and elevation. A geomorphic unit, substrate and flood imprint was derived for each plot in a GIS by considering the proportional area of the plot contributed by a dominant geomorphic unit, substrate or flood imprint type. If a plot was occupied by > 70% of a certain geomorphic unit or substrate and > 60% of a flood imprint type, then that geomorphic unit, substrate or flood imprint type was assigned to the plot. Plots not dominated by any certain geomorphic unit, substrate or flood imprint were deleted from the data set. In the geomorphic unit patch, 7 plots were deleted from the herbaceous data and 65 from the woody data, retaining 96 and 93% of total plant abundance respectively. In the substrate patch, 11 plots were deleted from the herbaceous data and 75 from the woody data, retaining 93 and 88% of total plant abundance. In the flood imprint patches, 24 plots were deleted from the herbaceous data and 167

Table 2
Summary of herbaceous and woody alien and native plant abundance and species richness in the Sabie River

	Abundance		Species richness	
	Number of individuals	% of total	Number of species	% of total
Herbaceous				
Alien	1463	6	19	16
Native	21,377	94	99	84
Total	22,840		118	
Woody				
Alien	306	3	9	7
Native	8547	97	127	93
Total	8853		136	

Total sampling area for the herbaceous vegetation is 3900 m^2 and for woody vegetation is 82,200 m^2.

Table 3
Alien plant species recorded on the Sabie River, indicating whether the species is invasive or naturalised and the manner of control

Species	Authority	Abu	Status	Controlled
Herbaceous				
Acanthospermum hispidum	DC.	3	Naturalized	No
Argemone ochroleuca	L.	2	Invasive	Slash/uproot
Bidens biternata	(Lour.) Merr. and Sherff	4	Naturalized	No
Bidens pilosa	L.	1	Naturalized	No
Cardiospermum halicacabum	L.	38	Invasive	Uproot
Catharanthus roseus	(L.) G. Don	43	Invasive	Uproot
Chenopodium album	L.	2	Naturalized	No
Commelina benghalensis	L.	102	Naturalized	No
Crotalaria agatiflora	Schweinf.	1	Naturalized	No
Flaveria bidentis	(L.) Kuntze	8	Naturalized	No
Pennisetum setaceum	(Forssk.) Chiov.	67	Naturalized	No
Persicaria lapathifolia	(L.) Gray	241	Naturalized	No
Pistia stratiotes	L.	681	Invasive	Biocontrol
Pupalia lappacea	(L.) A. Juss.	32	Naturalized	No
Senna occidentalis	(L.) Link	15	Invasive	Cut-stump/herbicide
Tagetes minuta	L.	22	Invasive	No
Tridax procumbens	L.	78	Naturalized	No
Waltheria indica	L.	56	Naturalized	No
Xanthium strumarium	L.	67	Invasive	Slash/uproot
Woody				
Caesalpinia decapetala	(Roth) Alston	1	Invasive	Cut-stump/herbicide
Chromolaena odorata	(L.) R.M. King and H. Rob.	3	Invasive	Cut-stump/herbicide
Cocculus hirsutus	(L.) Diels	3	Naturalized	No
Lantana camara	L.	201	Invasive	Cut-stump/herbicide
Melia azedarach	L.	6	Invasive	Cut-stump/herbicide
Ricinis communis	L.	4	Invasive	Cut-stump/herbicide
Senna didymobotrya	(Fresen.) Irwin and Barneby	8	Invasive	Cut-stump/herbicide
Senna septemtrionalis	Willd.	7	Invasive	Cut-stump/herbicide
Sesbania punicea	(Cav.) Benth	73	Invasive	Biocontrol

Authority- following Germishuizen and Meyer (2003).
Abu- Abundance.
Status- Current status of alien plants in KNP (terms follow Pyšek et al., 2004).

from the woody data, retaining 81 and 82% of total abundance respectively.

The plots belonging to each category within a patch type were used to calculate mean density and species richness of alien and native woody and herbaceous vegetation. One-way ANOVA was used to examine differences in density and species richness, using the categories within a patch (Table 1) as treatments. Sample sizes are unbalanced among treatments because of the complex morphology of the river channel, where different numbers of plots occurred in different zones, channel types, elevations, geomorphic units, substrates and flood imprints.

To examine the influence of the patches on individual alien species we used regression tree models. We only analysed 12 selected species for which there were more than 20 records across all 12 transects. Tree-based models provide an alternative to linear and additive logistic models for regression analysis (Breiman et al., 1984; Vayssieres et al., 2000). Regression tree models successively split data to form homogeneous subsets, resulting in a hierarchical tree of decision rules useful for exploring interactions between variables. We used S-Plus 2000 Professional Release 3 (MathSoft Inc., 2000) for fitting and examining the regression trees. The number of nodes was limited to 5 as our primary interest was to identify the main patches (response variables) structuring alien plant invasion patterns in the Sabie River, KNP. We then used the response prediction model to determine the percentage agreement (model fit) between our data and the results of the tree model, for species density.

3. Results

The abundance and species richness of alien plants in the Sabie River, at least inside the KNP boundary, is very low when compared to the abundance and species richness of native plants, comprising only 6% of the total herbaceous plant abundance and 3% of the total woody plant abundance respectively (Table 2). Alien plant species richness represented 16% of total herbaceous species richness and 7% of total woody species richness (Table 2). Of the alien plants that were found, most occurred in low numbers, with only one woody species and three herbaceous species having more than 100 records across all 12 transects (Table 3). Nine woody alien species were recorded during the survey, comprising only one naturalized species, but eight invasive species (Table 3). In contrast, 19 herbaceous alien species were recorded, with seven species considered invasive and the rest naturalized (Table 3).

In all six patches, there is an order of magnitude difference between native and alien plant density, for both herbaceous and woody vegetations (Figs. 3–8), indicating that native plants are numerically dominant in the post-flood river landscape. Similarly, in all patches, alien plant species richness is always markedly lower than native plant species richness. One anomaly was observed, where alien and native woody species abundance and richness is the same in the stayed physical flood imprint type. The stayed physical imprint type predominantly occurs at low areas of the channel (M. Parsons, unpublished data) and is therefore probably frequently disturbed.

Although the herbaceous alien plants showed some differences in density and species richness between patch types, there was only a significant difference in herbaceous density and species richness among geomorphic units (Fig. 7). Herbaceous alien plant density was almost an order of magnitude higher in the bedrock distributary and braid bar geomorphic units than in the other units, while species richness was highest in the braidbar geomorphic unit (Fig. 7).

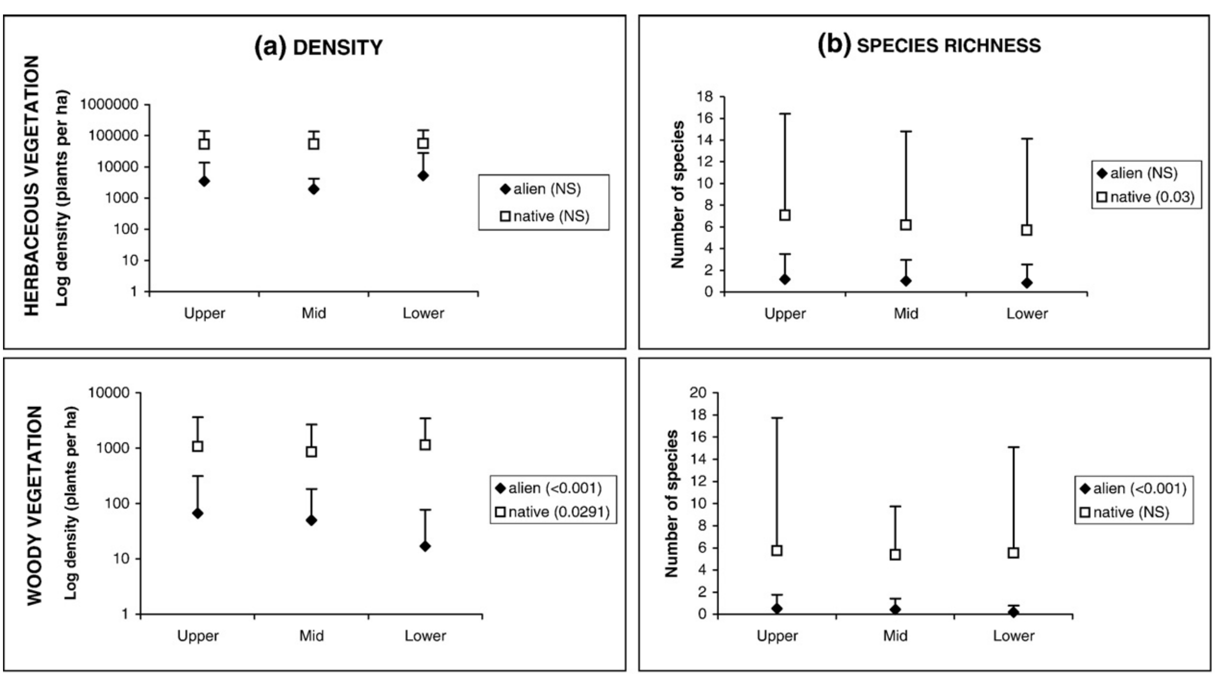

Fig. 3. Alien and native plant density (a), and species richness (b), in upper, mid and lower zones. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

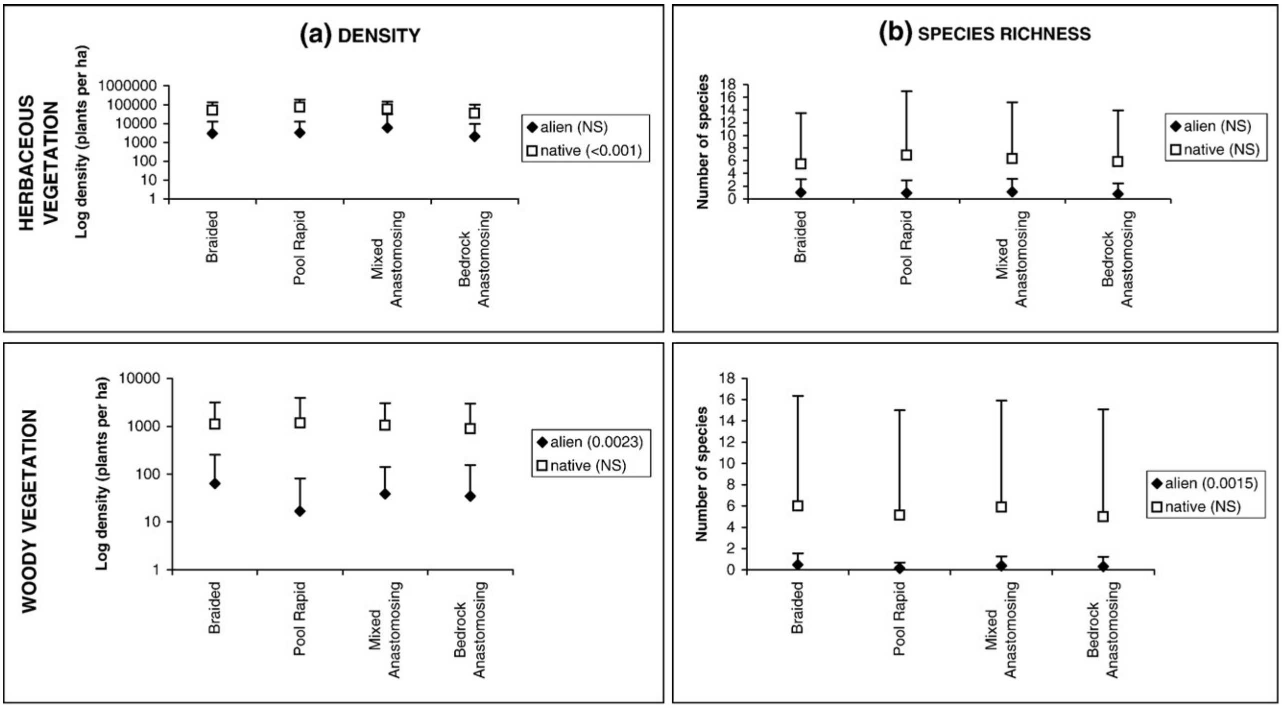

Fig. 4. Alien and native plant density (a), and species richness (b), in braided, pool rapid, mixed anastomosing, and bedrock anastomosing channel types. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

There was a significant difference in woody alien density and species richness among zones (Fig. 3), channel types (Fig. 4), and geomorphic units (Fig. 7). There were no differences in woody alien plant density among elevations (Fig. 5) or in woody alien plant species richness among flood imprints (Fig. 6). Woody alien density and species richness is highest in the upper and mid zones (Fig. 3). Woody alien species are significantly lower in both density and richness in the pool rapid channel type, while the braided, mixed anastomosing and bedrock anastomosing channel types have similar density and species richness (Fig. 4). Although not significantly different among elevations, woody alien plant density and species richness was highest in the

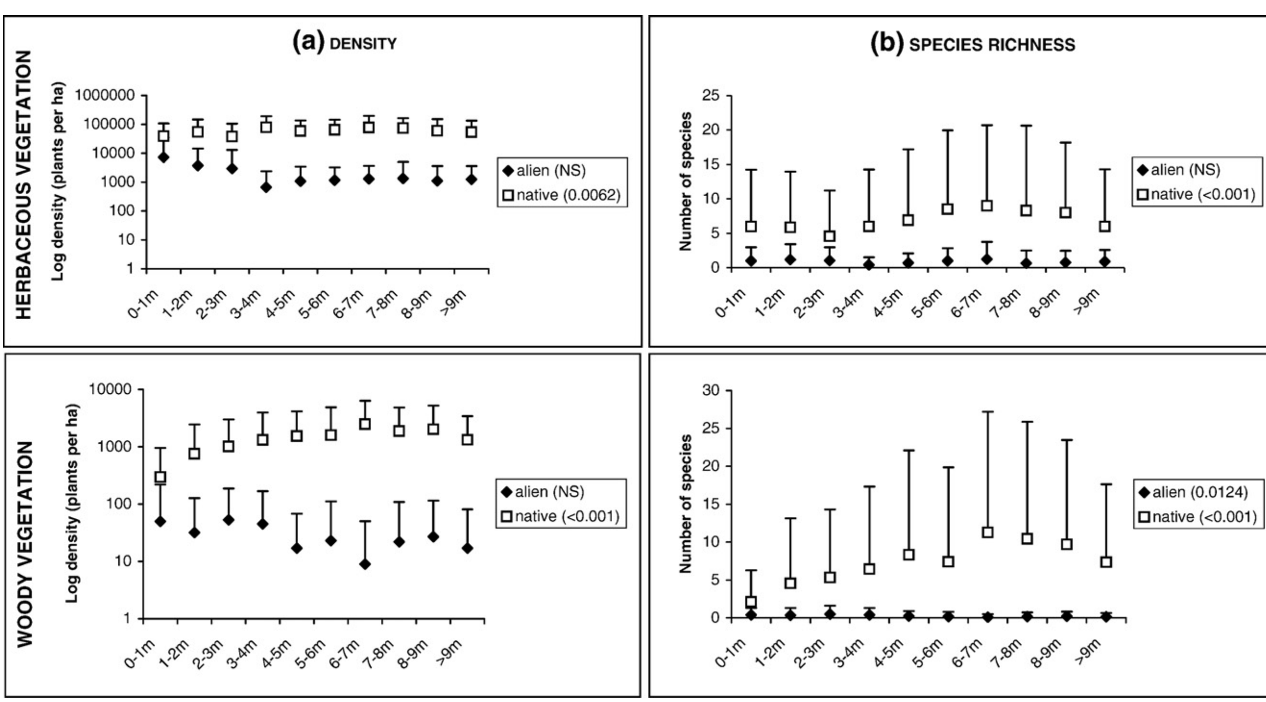

Fig. 5. Alien and native plant density (a), and species richness (b), in 1-m elevation intervals. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

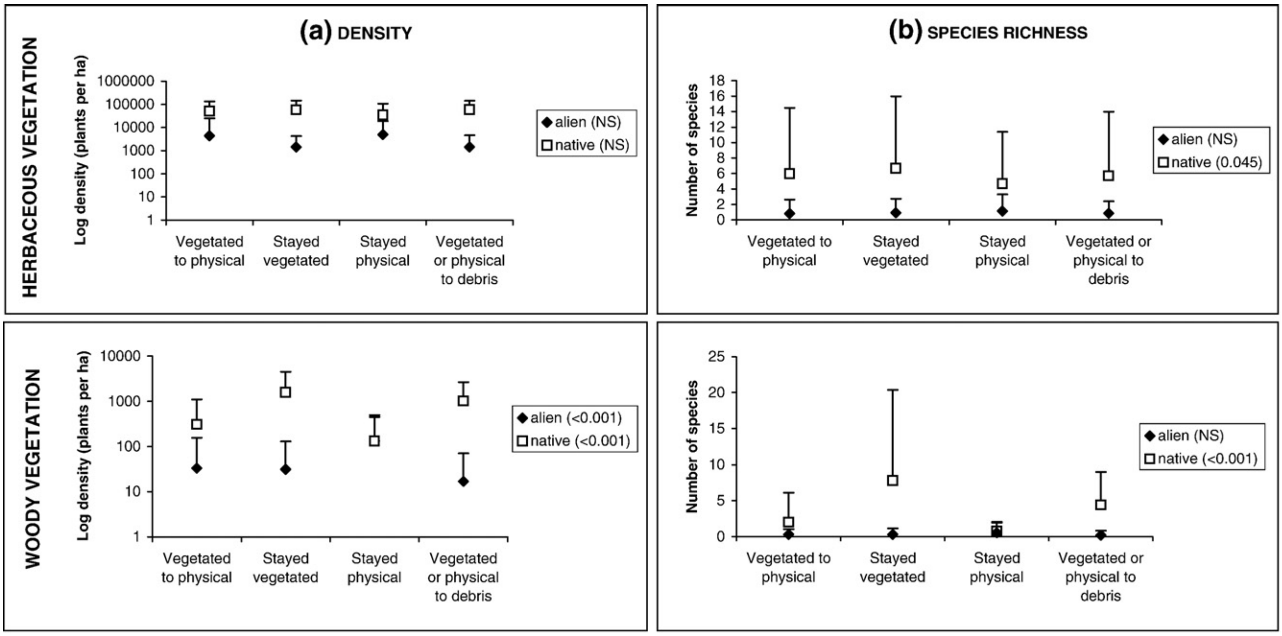

Fig. 6. Alien and native plant density (a), and species richness (b), in vegetated to physical, stayed vegetated, stayed physical and vegetated or physical to debris flood imprint types. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

braid bar geomorphic unit, with almost equal distribution of density and species richness across the other geomorphic units (Fig. 7). Woody alien species richness was highest below an elevation of 3 m, which is in contrast to native woody species richness which increases steadily up to an elevation of 7 m. Similarly, woody alien plant density was highest in the stayed physical flood imprint type, while the vegetated to physical and stayed vegetated flood imprint types had equal density, and the

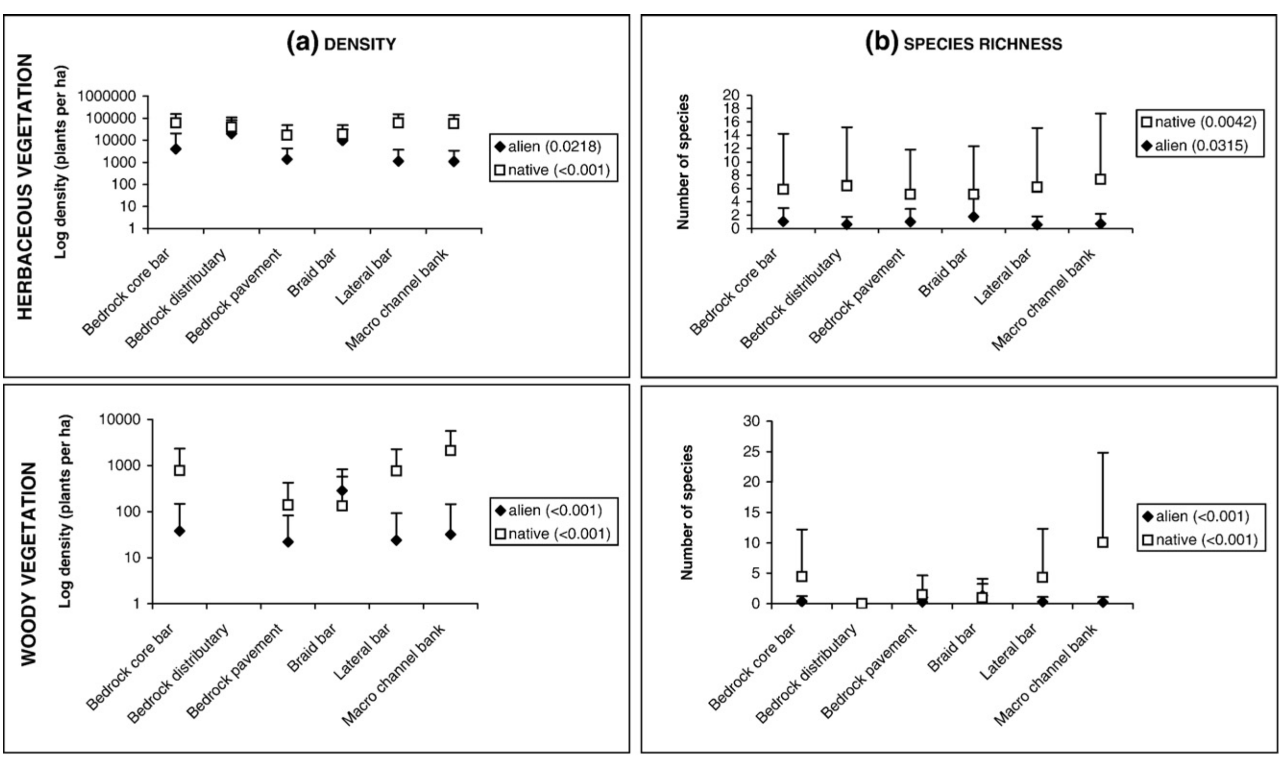

Fig. 7. Alien and native plant density (a), and species richness (b), in bedrock core bar, bedrock distributary, bedrock pavement, braid bar lateral bar, and macro-channel bank geomorphic units. Significant differences among groups are given in brackets in the figure legend. The bedrock distributary geomorphic unit does not contain any woody vegetation. Bars indicate Standard Deviation.

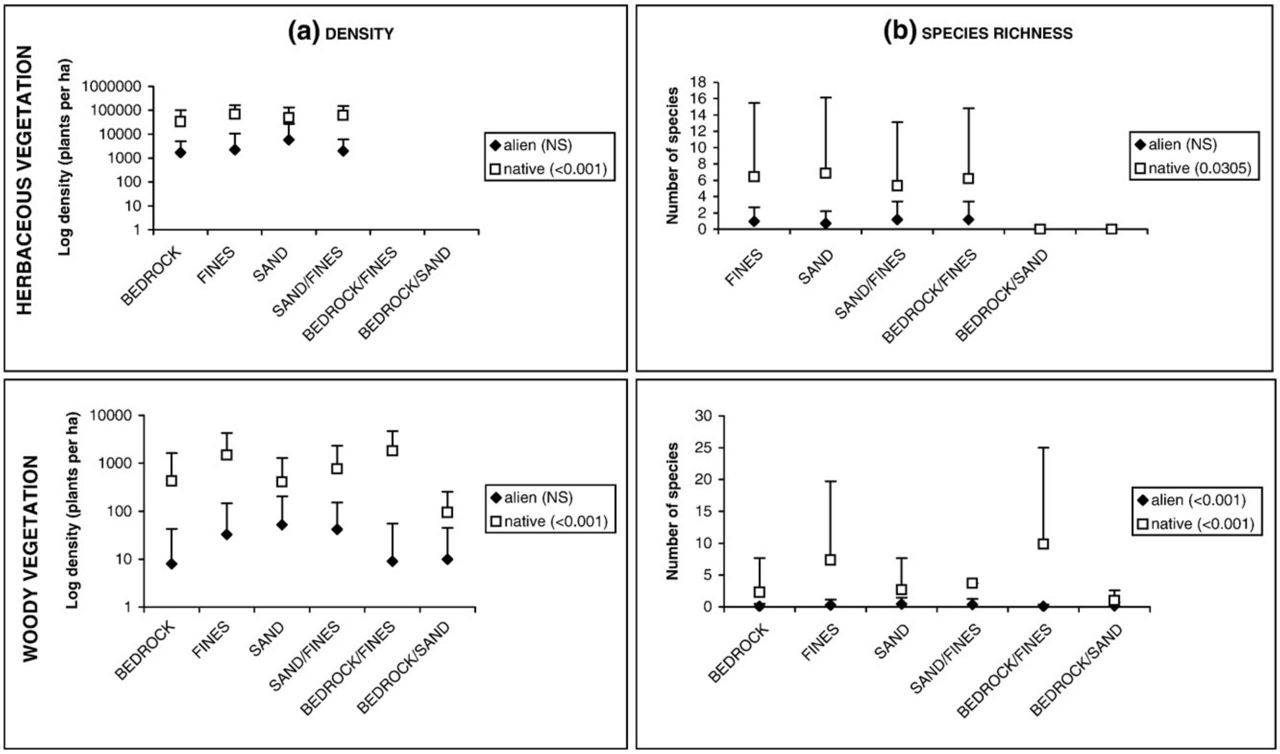

Fig. 8. Alien and native plant density (a), and species richness (b), in bedrock, fines, sand, sand/fines, bedrock/fines, and bedrock/sand substrates. Significant differences among groups are given in brackets in the figure legend. Bars indicate Standard Deviation.

vegetated or physical to debris flood imprint type the lowest. Woody alien species richness was highest on sand substrates, and lowest on the bedrock and bedrock/fines substrates.

Two woody species (*L. camara* and *Sesbania punicea*) and 10 herbaceous species (Table 4) were analysed using regression tree analysis (Fig. 9; *S. punicea*, for an example), to determine the main patch type (variable) influencing the pattern of that species (Table 4). The percentage agreement between the data and the fitted model varied from 78% to 95% (Table 4). *L. camara* appears to have responded primarily to the flood imprint type, with the highest abundance being recorded in vegetated to physical, stayed vegetated or vegetated or physical to debris flood imprint types. The lowest density of *L. camara* was found in the stayed physical flood imprint type, as well as between 0–2 m elevation and >4 m elevation. *S. punicea* responded mainly to geomorphic units, and was found in high density in braid bars, below an elevation of 1 m. *Cardiospermum halicacabum* responded in a similar manner to *L. camara*, being found in high density in the same disturbance patch types. The response of *C. roseus* to elevation was slightly unclear, but it appears that the highest abundances were found between an elevation of 1–7 m. *Commelina benghalensis* responded mainly to substrate, with highest abundances on rock, sand and fine substrates, and not on the combined substrates. *Pennisetum setaceum* responded solely to geomorphic units, being found in abundance only on braid bars and in low abundance in all other units. *Persicaria lapathifolia* responded similarly, but was found on braid bars, lateral bars and bedrock core bars in high abundance. *Tagetes minuta* was found in high abundance on sandy substrates, in the bedrock anastomosing and pool rapid channel types. *Tridax procumbens* was found in highest abundance between an elevation of 1–3 m, and in low abundance in all other elevations. *Waltheria indica* also responded primarily to elevation, and while not entirely clear, appears to be found in high abundance in the mid elevation ranges. Although *Xanthium strumarium* responded to flood imprint type, this response is unclear as high densities of *X. strumarium* were found in the stayed physical, vegetated to physical, vegetated or physical to debris flood imprint types. However, *X. strumarium* is also found in the upper zone, at low elevation in high abundance. Thus, individual woody and herbaceous alien plant species are associated with different patch types in the Sabie River landscape.

4. Discussion

Our hypothesis of patches acting as barriers in the river landscape is supported. Some patches contained higher density and richness of alien plants, indicating that these locations in the river landscape offer the resources necessary for alien plant establishment. Density and species richness of herbaceous alien plants appear to be strongly associated with geomorphic units in the Sabie River. This was supported by a number of species which indicated geomorphic units to be the main driver of distribution. In particular, the braid bar geomorphic unit appears to be particularly important. Braid bars are characteristically eroded and reformed during major floods (Heritage and Moon, 2000), through accumulation of unconsolidated sediment. It is

Table 4
Response of selected alien plants to patch type, as suggested by the regression tree analysis (see Fig. 9 for an example)

Species	Number of records	Main response variable (patch type)	Response: High abundance	Response: Low abundance	% agreement abundance (plants/ha)	Management type
Woody						
Lantana camara	201	Flood imprint	Vegetated to physical, stayed vegetated, vegetated or physical to debris.	All flood imprint types except for those indicated in the high abundance column, and, elevation between 0–2 m, >4 m.	78	Cut-stump treatment
Sesbania punicea	73	Geomorphic unit	Braid bar, and, at an elevation of <1 m.	All geomorphic units except for braid bar, and, at elevations of >1 m.	94	Biological control
Herbaceous						
Cardiospermum halicacabum	38	Flood imprint	Vegetated to physical, stayed vegetated, vegetated or physical to debris.	All flood imprint types except for those indicated in the high abundance column, and, elevation between 0–2 m, >4 m, and, on all channel types except for braided bar and macro-channel bank/ bedrock core bar.	85	Uprooting
Catharanthus roseus	43	Elevation	At elevations between 1–3 m, 4–5 m, 6–7 m, and, on braided channel types.	At elevations of 0–1 m, 3–4 m, 5–6 m and >7 m.	92	Uprooting
Commelina benghalensis	102	Substrate	On rock, sand and fine substrates, and, on flood imprint types of vegetated or physical to debris, vegetated to physical, or stayed vegetated.	On all combinations of substrates, except for those indicated in the high abundance column.	78	None
Pennisetum setaceum	67	Geomorphic unit	Braid bar units.	All other geomorphic units.	95	None
Persicaria lapathifolia	241	Geomorphic unit	Braid bar, lateral bar, bedrock core bar.	All other geomorphic units.	78	None
Pupalia lappacea	32	Elevation	Elevation of 3–4 m, 5–6 m, >8 m, and, fine substrate, and, in the mid zone.	Elevation of 0–3 m, 4–5 m, 6–8 m.	92	None
Tagetes minuta	22	Substrate	Sand substrate, and, flood imprint types of vegetated to physical, stayed vegetated or stayed physical, and, in bedrock anastomosing and pool rapid channel types.	Elevation of 0–5 m, >6 m.	95	Uprooting/ slashing
Tridax procumbens	78	Elevation	Elevation of 1–3 m, and, patch types of vegetated to physical, stayed vegetated and vegetated or physical to debris, and, substrate of sand or sand/fines.	Elevation of 0–1 m, >3 m.	81	None
Waltheria indica	56	Elevation	Elevation of 4–5 m, 6–8 m, >9 m, and, in the lower zone, and, in bedrock anastomosing and mixed anastomosing channel type.	Elevation of 0–4 m, 5–6 m, 8–9 m.	87	None
Xanthium strumarium	67	Flood imprint	Flood imprint types of stayed physical, vegetated to physical, vegetated or physical to debris, and, in the upper zone, and, at elevations of 1–2 m.	On all other flood imprint types and combinations thereof.	93	Uprooting/ slashing

The main response variable is the variable (patch type) that is responsible for the first split in regression tree. The % agreement was determined using the response prediction model to determine the percentage agreement (model fit) between our data and the results of the tree model.

most likely that alien plant propagules are deposited in the sediments of the newly formed (thus disturbed) bars, and are able to colonize these areas quickly. The response of alien plants to flood imprints is however not very clear, as there was no preference to either the stayed physical, vegetated to physical, vegetated or physical to debris flood imprint types. It does appear though that some alien plant species were more frequently found in patches of woody debris, matching the response found by Pettit and Naiman (2006) who report higher abundance and richness of seedlings taken from soil under debris piles in comparison to the surrounding area. This is not surprising, as the debris piles would provide protection to seedlings and increased surface detritus and nutrients from the accumulated decomposing material (Pettit and Naiman, 2005).

To gain further insight into the roles of patches in the landscape as barriers to alien plant invasion, the similarities and contrasts of both the trends in alien plant density and richness, as well as trends of the individual species, should be compared. Although trends in alien plant density and richness broadly indicate preferences of herbaceous and woody life forms for certain patches, individual alien species are more clearly associated with different patches. This indicates that some patches act as barriers to the invasion of individual species in the river landscape. However, the variation and standard deviations for density and species richness across all the patches indicates a high degree of variability in the system. This may indicate the inherent variability of plant distribution in the river landscape. The higher species richness and density of alien

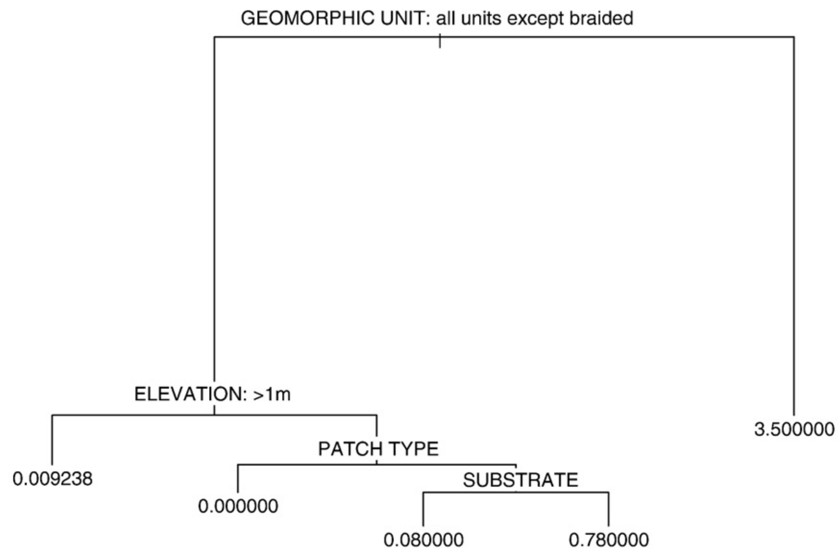

Fig. 9. Regression tree of *Sesbania punicea* abundance along the Sabie River. Rules indicated on top of each splitting branch apply to the left branch. Values at terminal nodes indicate the predicted density (plants/ha). The variable at the top of the tree represents the most important variable by which the data is successively split to form the homogenous groups at the terminal nodes.

plants at lower elevations (0–3 m), although only significant for herbaceous species, is probably an indication of the higher frequency of disturbance by subsequent flows at lower elevations in the river channel. However, when viewed at the species level, except for *S. punicea* which has higher abundances below 1 m, the response of individual species to elevation is not very clear. This possibly means that *S. punicea* invasion is facilitated by the conditions provided at low elevations in the channel, perhaps more frequent inundation or disturbance. However, it is also interesting to note that native species richness is also lowest in the disturbed conditions at lower elevations. Clearly, patchiness or gaps in the system provide for increased invasion ability (With, 2002). However, no work has assessed the response of individual species to a range of potential barriers present in a particular system. The specific traits of each alien species will influence the degree to which it is associated with different patch types, and thus the degree to which certain patches then act as barriers to invasion. This will most likely be a product of the dispersal mode and propagule production, defence mechanisms, resource demands, competitiveness, seed banking strategies and seed size of each species. Thus, individual species invasions are associated with different parts of the river landscape following a large flood.

Two additional factors may be important barriers for the establishment of alien species in the Sabie River landscape. These are the management programme (clearing by Working for Water teams) and the richness and density of native vegetation in the landscape. Alien plants currently represent a small percentage of the total plant abundance and species richness in the Sabie River within KNP, and half of the species we recorded are controlled either mechanically/chemically or biologically (Table 3). The fact that less than 6% of the total plant abundance comprises alien species may indicate the effectiveness of the clearing programme. The low abundance of alien plants is thus either a limitation of the study or an indication of the barriers to species establishment in the system. However, the low abundance of alien plants might be an important strength of the study as well, as this represents the situation as is currently experienced in an area that is receiving ongoing management, and perhaps, the current population of alien plants might then represent preferential areas for growth and which supply sufficient resources to allow rapid re-colonisation. It also appears that the high native species abundance and richness might be playing an important role in maintaining invasions at low level. Parsons et al. (2005) reported that 75% of woody plant abundance in the post-flood landscape was contributed by plants that established after the flood and 25% by residual plants that survived the flood. The presence of relatively high abundances of both newly established and residual native plants in the Sabie River landscape may exert competitive influences on alien plants. Although there is a vast literature that both supports and contradicts the competitive role of native vegetation viewpoint (for example, Kennedy et al., 2002; Stohlgren et al., 2003), there is clearly a substantial difference in abundance between alien and native vegetation along the Sabie River. This warrants further investigation, probably at multiple spatial scales, before the effect of native species richness on alien plants is better understood.

Overall, alien plants represented a small proportion of the vegetation in the Sabie River landscape after the 2000 flood. Given the propagule pressure from outside the park, this is perhaps unusual. The slight trend of decreasing density and richness between the upper, mid and lower zones of the Sabie River indicates the importance of propagule pressure in the watershed to the west of KNP, agreeing with other studies that have highlighted this area as a major source of invasion for the lower reaches (Foxcroft et al., 2007; Beater et al., 2008-this issue; Witkowski and Garner, 2008-this issue). The failure of many alien plant species to establish after the 2000 flood is likely due to a combination of factors—the plant specific barriers imposed by the structure and pattern of patches in the landscape, the high abundance and richness of native vegetation leading to competition, and for some species certainly, the clearing operations.

If management was only concerned with one species, it is likely that the barriers and promoters of invasion could be determined, and priority areas mapped accordingly. However, where multiple species are concerned and the removal of one species may result in replacement by another alien species, a more holistic approach is needed. For example, overall, the braid bar is an important patch for most species. However, it does not appear to be at all important for *L. camara*, which remains a high priority species in the KNP. The most important consideration for managers controlling alien plants then might be to determine which areas of the landscape patch mosaic are most likely to be invaded by 1) a suite of invasive plants, the combined effect of which might be particularly harmful, and 2) aggressive species which might occur over a wider area, and then determine what indigenous species are likely to be impacted in these highly invaded areas.

We have taken a new approach to elucidate patterns of alien plant invasion by considering the river landscape as patches that may act as barriers to the establishment of alien plants after a large flood disturbance. We have shown that different densities, species richness and individual alien plant species occur in different patches in the Sabie River landscape following a large flood. Management strategies of largely natural systems such as KNP should be based on an understanding of alien species distributions and preferences for patches in the river landscape. Managing for plant invasions at places in the landscape that alien plants do not have a preference for, and without consideration of the ways that patches may act as barriers to invasion, can be wasteful of resources and may allow invasions to progress rather than be inhibited.

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