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Impact of alien trees on mammal distributions along an ephemeral river in the Namib Desert

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Abstract

Ephemeral rivers and the vegetation they support have numerous ecological and economic values to the mammals and people who rely on these systems. Yet, these crucial environments are believed to be threatened by exotic plant invasion. In Africa, invasive trees of the genus *Prosopis* have detrimental effects on native vegetation, bird and dung beetle communities; however, to date, there is no evidence that *Prosopis* establishment has affected indigenous wild mammalian distribution and ecology in its introduced range. Using a combination of camera traps and vegetation surveys, we tested the hypothesis that *Prosopis* invasion has a negative impact on the mammals of the ephemeral Swakop River in Namibia by reducing mammal species richness and species occupancies. *Prosopis* was found to have no negative impact on species richness; however, evidence for species-specific responses to *Prosopis* abundance was found. This is the first study to confirm an impact of *Prosopis* on sub-Saharan African mammals, providing a foundation for future research and the development of appropriate management policy.

Key words: camera traps, drylands, invasive, *Prosopis*, riparian, wildlife

Résumé

Les cours d'eau éphémères et la végétation qu'ils supportent représentent de nombreuses valeurs écologiques et économiques pour les personnes et les mammifères qui dépendent de ces systèmes. Mais on estime que ces environnements cruciaux sont menacés par l'invasion de plantes exotiques. En Afrique, les arbres invasifs du genre *Prosopis* ont des effets destructeurs sur les communautés de végétation, d'oiseaux et de bousiers indigènes. Pourtant, à ce jour, il n'existe pas de preuve que l'installation des *Prosospis* ait affecté la distribution et l'écologie des mammifères sauvages indigènes dans les zones où il a été introduit. Utilisant conjointement des pièges photographiques et des études de la végétation, nous avons testé l'hypothèse selon laquelle l'invasion de *Prosopis* aurait un effet négatif sur les mammifère du fleuve Swakop, en Namibie, parce qu'elle réduirait la richesse en espèces de mammifères et l'aire occupée par les espèces. Il s'est avéré que *Prosopis* n'avait aucun impact négatif sur la richesse en espèces, mais on a trouvé des preuves de réponses spécifiques par espèce à l'abondance des *Prosopis*. Ceci est la première étude qui confirme l'impact des *Prosopis* sur des mammifères d'Afrique subsaharienne; elle constitue une base pour de futures recherches et pour le développement de politiques de gestion appropriées.

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Introduction

Ephemeral rivers are a unique feature of arid landscapes: their episodic flow and constant groundwater supports riparian vegetation, which is distinct from the surrounding landscape (Jacobson, Jacobson & Seely, 1995). As a result, they are often referred to as linear oases and are used by people and wildlife for a variety of purposes (Seely *et al.*, 2003). Mammals, in particular, use these habitats as dispersal corridors, allowing them to travel through otherwise inhospitable areas (Coetzee, 1969). These mammalian populations have a tremendous importance for both people's livelihoods and national economies (Richardson, 1998). Unfortunately, ephemeral rivers and the species they support are faced with numerous threats, one of which being alien invasive tree species.

Exotic plant invasions are known to reduce native plant species richness and alter ecosystem functioning (Bethune, Griffin & Joubert, 2004; Hejda, Pyšek & Jarošik, 2009). Interestingly, comparatively fewer studies have assessed the impacts of invasive plants on native fauna (Pyšek *et al.*, 2012). Invasive plants have a bottom-up effect on higher trophic levels (Vilà *et al.*, 2011) and can impact wildlife communities by altering the characteristics of their environment such as vegetation structure, resource quality and habitat diversity (Mills & Retief, 1984; Ferdinands, Beggs & Whitehead, 2005; Valentine, Roberts & Schwarzkopf, 2007). Predicting the outcome of tree invasions can be difficult as it is dependent on both the traits of the invasive plant and the attributes of the native environment (Pyšek *et al.*, 2012); previous studies have revealed inconsistencies of the effect invasive plants can have on native wildlife (Valentine, Roberts & Schwarzkopf, 2007; Pearson, 2009).

Plants of the genus *Prosopis* L. are invasive species of global concern due to their aggressive nature in introduced ranges, the effects their dense stands have on water resources and the detrimental impact their introduction has had on open grasslands and woodland ecosystems (Global Invasive Species Database; www.issg.org). For example, *Prosopis* establishment has had a negative effect on the herbaceous community of the Turkwel riverine forest, Kenya, by reducing herbaceous plant density and diversity (Muturi *et al.*, 2013). In South Africa, *Prosopis* has been shown to lower avian diversity (Dean *et al.*, 2002) and dung beetle species richness (Steenkamp & Chown, 1996). In the Allideghi Wildlife Reserve, Ethiopia, the reduction of herbaceous vegetation cover and species richness in grassland ecosystems due to *Prosopis* invasion, is thought to have negative implications for wild ungulates in the area, forcing them into less favourable habitats (Kebede, 2009). Whilst there are predictions about the potential negative effect of *Prosopis* on wild mammals (Kebede, 2009), there is no conclusive evidence that *Prosopis* has impacted native mammals in its introduced range.

The aim of this study is to explore what impact, if any, the presence of the invasive tree *Prosopis* is having on mammals along an ephemeral river in Namibia. Mammals are extremely important to Namibia's economy, where wildlife assets are worth US\$1.26 billion and wildlife viewing is a valuable contributor to the country's economy (MET, 2010). *Prosopis* is regarded as the terrestrial invasive species of greatest concern in Namibia and as the biggest threat to riparian woodlands along the country's ephemeral rivers (Bethune, Griffin & Joubert, 2004; Joubert, 2009). The species has been associated with increased mortality and reduced species richness of native woodlands (Vinjevold, Bridgeford & Yeaton, 1985; Bethune, Griffin & Joubert, 2004; Mannheimer & Curtis, 2010). From these changes to the riparian vegetation upon which wildlife relies and previous studies which have revealed the negative impact of *Prosopis* introduction on wildlife (Steenkamp & Chown, 1996; Dean *et al.*, 2002), we hypothesize that the presence of *Prosopis* should have a negative impact on mammals within the Swakop River region at (i) the community level, by reducing mammal species richness; and (ii) the individual level, by lowering the occupancy probabilities of certain mammal species.

Materials and methods

Study area

Our study takes place along the 93 km stretch of the Swakop River, one of Namibia's twelve major ephemeral rivers, that flows through the Namib-Naukluft National Park in the central Namib Desert. The river consists of sandy alluvium, which is dry for most of the year with only occasional flows in the summer months. The riparian woodland community is largely composed of native *Faidherbia albida* (Delile) A. Chev., *Acacia erioloba* E. Mey., *Acacia tortilis* Hayne, *Euclea pseudebenus* E. Mey., *Salvadora persica* L., and *Tamarix usneoides* E. Mey., and the invasive *Prosopis* species L. (Jacobson, Jacobson & Seely, 1995). The riparian vegetation provides resources such as food, shelter and shade: low levels of grass cover (median 5%, range 0–30%) were observed, so woody vegetation is thought to be the primary resource for wildlife within the river. Strict regulations on human activity are maintained within the park: no human settlement is allowed, camping is only permitted in designated locations, and vehicle traffic is restricted to designated roads during daylight hours.

Prosopis was first introduced to Namibia in 1912 (Smit, 2004). The *Prosopis* invasion on the Swakop River is thought to be the most severe of all of Namibia's major ephemeral rivers (Tarr & Loutit, 1985; Brown & Gubb, 1986; Macdonald & Nott, 1987; Henschel & Parr, 2010). Six *Prosopis* species have been successfully introduced, and widespread hybridization is believed to have occurred between them (Smit, 2004). Owing to this hybridization, this study does not attempt to differentiate between species and uses the genus name of *Prosopis*. The three most common species found in Namibia's rivers are *P. glandulosa var torreyana, P. chilensis* and *P. velutina* (Smit, 2004).

Animal data

Thirteen Rapidfire RC55 camera traps (Reconyx Inc., Holmen, WI, U.S.A.) were placed in riparian woodlands at 7 km intervals along the dry riverbed. The first camera trap was placed at 22°41′S and 14°55′E and the thirteenth camera trap at 22°38′S and 15°30′E. The camera traps were operational during the dry austral winter of 2010 (from 23/07/10 until 8/11/10). The sampling period is towards the end of the dry winter season, and due to the scarcity of vegetation and water sources outside of the river at this time of year, the wildlife's reliance on this ecosystem is at its greatest. Camera traps were fitted to stakes, at a height of 45 cm, positioned at a random location and orientation in each woodland.

Environmental data

Data on vegetation 500 m upstream and downstream of each camera trap were collected at the patch level, where patches were defined as trees of the same species with a shared canopy. These data were (i) species identity; (ii) canopy dieback (percentage of the canopy composed of dead branches and grouped into categories: ≤24%; 25–49%; 50–74%; and ≥75%); (iii) vegetation height (categories: <2 m; 2–4.5 m; 5–7.5 m; and ≥8 m); and (iv) canopy height [categories: ground; low (<0.5 m); medium (0.5–1.5 m); and high (>1.5 m)] (Table 1). The number of native tree patches and *Prosopis* patches were counted to determine the abundance of *Prosopis* at each camera trap location. Density, as opposed to cover, was chosen as the best way to characterize the vegetation at each camera trap because trees tended to grow in discrete patches. Patch density as opposed to stem density was used as the latter leads to biased estimates favouring species that have multiple small stems as opposed to single large stems.

Statistical analyses

To determine which mammal species use the dry river bed during the austral winter, a species inventory was compiled from the camera trap data. Photographic rates were calculated for each species detected; any photograph of the same species triggered within an hour was considered to be the same individual and discounted (Tobler *et al.*, 2008).

Species detection histories based on presence/absence data at each camera trap were compiled and used to inform species richness and occupancy analyses (Linkie *et al.*, 2007; de Wan *et al.*, 2009). The total number of days the camera traps were active (from 23/07/10 until

Table 1 Summary of vegetation characteristics (canopy dieback, vegetation height and canopy height) for each camera trap along the ephemeral Swakop River in the Namib-Naukluft National Park

Camera trap	*Prosopis* abundance	Median canopy dieback	Median vegetation height	Mode canopy height
1	Low	50–74% (level 3)	2.0–4.5 m (level 2)	<0.5 m (level L)
2	Low	50–74% (level 3)	2.0–4.5 m (level 2)	<0.5 m (level L)
3	High	25–49% (level 2)	2.0–4.5 m (level 2)	<0.5 m (level L)
4	High	25–49% (level 2)	2.0–4.5 m (level 2)	<0.5 m (level L)
5	Low	25–49% (level 2)	2.0–4.5 m (level 2)	<0.5 m (level L)
6	High	<24% (level 1)	2.0–4.5 m (level 2)	<0.5 m (level L)
7	High	25–49% (level 2)	2.0–4.5 m (level 2)	<0.5 m (level L)
8	High	<24% (level 1)	2.0–4.5 m (level 2)	<0.5 m (level L)
9	High	25–49% (level 2)	2.0–4.5 m (level 2)	<0.5 m (level L)
10	Low	25–49% (level 2)	5.0–7.5 m (level 3)	0.5–1.5 m (level M)
11	Low	<24% (level 1)	2.0–4.5 m (level 2)	0.5–1.5 m (level M)
12	Low	25–49% (level 2)	2.0–4.5 m (level 2)	0.5–1.5 m (level M)
13	Low	25–49% (level 2)	2.0–4.5 m (level 2)	0.5–1.5 m (level M)

8/11/10) were grouped into approximately 10-day sampling occasions to improve the chances of detecting species within each sampling occasion, resulting in eleven occasions (Olea & Mateo-Tomás, 2011).

Species richness analysis was conducted using EstimateS (Colwell, 2006). Species detection histories at each camera trap were grouped on the basis of high or low *Prosopis* abundance. If *Prosopis* presence exceeded 35% of the total vegetation surveyed at each camera trapping location, the area was considered a *Prosopis* abundant area. This threshold was selected as it allowed for an equal sampling effort between areas of high and low *Prosopis* abundance (the mean percentage *Prosopis* density across the camera trap locations was 37%).

Species richness curves were created using sample-based rarefaction curves (Colwell, Mao & Chang, 2004). First-order Jackknife was used as a nonparametric species richness estimator as it produces accurate true species richness estimates for small sampling effort (Hortal, Borges & Gaspar, 2006) and as this type of estimator was previously shown to perform well with camera trapping data (Tobler *et al.*, 2008). The units were rescaled from samples to individuals through EstimateS to ensure that the results represent species richness as opposed to species density (Gotelli & Colwell, 2001). The Wilcoxon rank-sum test was used to infer whether the Jackknife species richness estimates significantly differed between areas of high and low *Prosopis* abundance.

Occupancy analysis was conducted using PRESENCE (Mackenzie, 2012). A single-season model was used and carried the following assumptions: sites are independent; there is no unexplained heterogeneity in the detection of species across the sites nor in the occupancy states; the sites are 'closed', and occupancy states are constant during the season (Conroy & Carroll, 2009). To avoid violating model assumptions, any heterogeneity in vegetation characteristics that might potentially affect detection probabilities (P) was modelled as site-specific

Table 2 Mammalian species inventory compiled from species detected by camera traps in the ephemeral Swakop River in the Namib-Naukluft National Park. Species are listed in the table by decreasing capture rate. Also presented are the photographic rate, presence in high or low Prosopis abundance (+) and the number of times the species was captured (n)

Species (common name: Order)	Scientific name	Photographic rate	High *Prosopis* abundance	Low *Prosopis* abundance
Steenbok: Artiodactyla	*Raphicerus campestris*	193: 0.152	+ (101)	+ (92)
Chacma baboon: Primate	*Papio ursinus*	141: 0.111	+ (109)	+ (32)
Gemsbok: Artiodactyla	*Oryx gazelle*	68: 0.054	+ (7)	+ (61)
Greater kudu: Artiodactyla	*Tragelaphus strepsiceros*	38: 0.03	+ (31)	+ (7)
Black-backed jackal: Carnivora	*Canis mesomelas*	32: 0.025	+ (19)	+ (13)
Common duiker: Artiodactyla	*Sylvicapra grimmia*	27: 0.021	+ (1)	+ (26)
Cape hare: Lagomorpha	*Lepus capensis*	25: 0.02	+ (10)	+ (15)
African wildcat: Carnivora	*Felis silvestris lybica*	21: 0.017	+ (14)	+ (7)
Klipspringer: Artiodactyla	*Oreotragus oreotragus*	16: 0.013	+ (11)	+ (5)
Springbok: Artiodactyla	*Antidorcus marsupialis*	10: 0.008	+ (4)	+ (6)
Muridae species: Rodentia:	Unknown	10: 0.008	+ (1)	+ (9)
Cape porcupine: Rodentia	*Hystrix africaeaustralis*	9: 0.007	+ (9)	
Mountain zebra: Perissodactyla	*Equus zebra*	6: 0.005	+ (2)	+ (4)
Honey badger: Carnivora	*Mellivora capensis*	5: 0.004		+ (5)
Striped polecat: Carnivora	*Ictonyx striatus*	4: 0.003	+ (3)	+ (1)
Caracal: Carnivora	*Caracal caracal*	2: 0.002	+ (1)	+ (1)
African civet: Carnivora	*Civettictis civetta*	2: 0.002	+ (1)	+ (1)
Yellow mongoose: Carnivora	*Cynictis penicillata*	1: 0.001		+ (1)
Hyrax: Hyracoidea	Most likely *Procavia capensis*	1: 0.001		+ (1)
Aardvark: Tubulidentata	*Orycteropus afer*	1: 0.001		+ (1)
Leopard: Carnivora	*Panthera pardus*	1: 0.001	+ (1)	
Warthog: Artiodactyla	*Phacochoerus africanus*	1: 0.001	+ (1)	
Cape ground squirrel: Rodentia	*Xerus inauris*	1: 0.001	+ (1)	
Total species = 23			Total species = 19	Total species = 19

covariates (Mackenzie *et al.*, 2002). Six models were developed to estimate *P* and ψ (occupancy). These models considered one potential covariate of ψ: *Prosopis* abundance, and two potential covariates of *P*: canopy height and dieback. Vegetation height was not included as a covariate, because it was found that the median levels were constant across the camera traps (2.0–4.5 m) with the exception of camera trap 10 (5.0–7.5 m) (Table 1). The latter covariates may influence *P* if, for instance, they affect species' movements. *Prosopis* abundance was modelled as a continuous covariate and standardized by z-transformation prior to analysis (Donovan & Hines, 2007). Canopy height and dieback were modelled as categorical covariates. The most appropriate model was chosen based on its AIC ranking (Burnham & Anderson, 2002).

Results

The camera traps were operational along the dry riverbed for an average of 97.6 days, resulting in a trapping effort of 1269 days. Camera traps detected 23 species representing eight mammalian Orders (Table 2). The species inventory shows that 19 species were detected in areas of both high and low *Prosopis* abundance. A closer inspection of the inventory reveals that although an equal number of species were found in both areas, the composition of species is not identical as some species were only detected in areas of high or low *Prosopis* abundance. For example, cape porcupine (*Hystrix africaeaustralis*) was only detected in *Prosopis* abundant areas, and honey badger (*Mellivora capensis*) was only detected in areas with a low *Prosopis* abundance.

Figure 1 displays the species richness curves for areas with high and low *Prosopis* abundance. Although the nonparametric species richness estimator, Jackknife, predicted a marginally greater number of species in areas of high, rather than low, *Prosopis* abundance (25 and 23 species; Fig. 1), no significant difference in species richness in areas of high and low *Prosopis* abundance could be established (Wilcoxon rank-sum test: $W = 53$, $P = 0.65$).

Occupancy analysis was originally performed on the 23 species where information was gathered, but 15 of these species had to be discounted due to the models failing and producing occupancy estimates of one. In 12 of these 15 cases, this was due to low detection probabilities across all sites, namely for the cape porcupine; mountain zebra (*Equus zebra*); honey badger; striped polecat (*Ictonyx striatus*); caracal (*Caracal caracal*); African civet (*Civettictis civetta*); yellow mongoose (*Cynictis penicillata*); hyrax (either *Heterohyrax brucei* or *Procavia capensis*); aardvark (*Orycteropus afer*); leopard (*Panthera pardus*); warthog (*Phacochoerus africanus*); and cape ground squirrel (*Xerus inauris*). In the remaining three cases, this was due to high detection probabilities across all sites, namely for steenbok (*Raphicerus campestris*); chacma baboon (*Papio ursinus*); and gemsbok (*Oryx gazelle*).

Eight species produced reliable occupancy estimates. Of these, three were not affected by *Prosopis*: greater kudu (*Tragelaphus strepsiceros*); black-backed jackal (*Canis mesomelas*); and klipspringer (*Oreotragus oreotragus*). Five species (Table 3), however, showed significant sensitivity

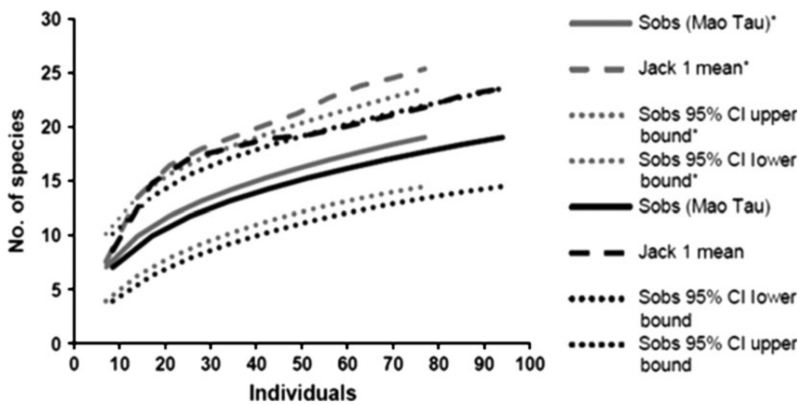

Fig 1 Mammal species richness curves for the ephemeral Swakop River in the Namib-Naukluft National Park. Both species observed (Mao Tau, with 95% confidence intervals) and nonparametric species richness estimator (first-order Jackknife) are provided for high *Prosopis* abundance areas (*) (i.e. >35% *Prosopis* density) and low *Prosopis* abundance areas (i.e. <35% *Prosopis* density)

Table 3 Occupancy estimates for the species affected by *Prosopis* abundance along the ephemeral Swakop River in the Namib-Naukluft National Park. Model selection was carried out by identifying models with the lowest AIC

		Occupancy estimates (standard error) for each species and the model of best fit				
Camera Trap	% *Prosopis* abundance	*S. grimmia*, ψ (% *Prosopis*) *P* (db)	*A. marsupialis*, ψ (% *Prosopis*) *P* (ch)	*F. s. lybica*, ψ (% *Prosopis*) *P* (.)	Muridae species, ψ (% *Prosopis*) *P* (ch)	*L. capensis*, ψ (% *Prosopis*) *P* (.)
1	24	0.834 (0.133)	0.755 (0.158)	0.428 (0.092)	0.331 (0.154)	0.519 (0.084)
2	22	0.864 (0.129)	0.784 (0.165)	0.418 (0.104)	0.309 (0.170)	0.522 (0.096)
3	46	0.241 (0.124)	0.310 (0.130)	0.551 (0.067)	0.622 (0.116)	0.487 (0.060)
4	72	0.012 (0.031)	0.044 (0.098)	0.688 (0.219)	0.871 (0.212)	0.449 (0.227)
5	34	0.587 (0.051)	0.561 (0.046)	0.484 (0.020)	0.462 (0.038)	0.504 (0.018)
6	55	0.094 (0.115)	0.171 (0.169)	0.600 (0.126)	0.728 (0.193)	0.474 (0.118)
7	68	0.020 (0.045)	0.061 (0.119)	0.669 (0.201)	0.845 (0.219)	0.454 (0.202)
8	40	0.406 (0.055)	0.434 (0.050)	0.517 (0.022)	0.541 (0.041)	0.496 (0.020)
9	69	0.018 (0.041)	0.057 (0.114)	0.673 (0.205)	0.852 (0.218)	0.453 (0.208)
10	16	0.932 (0.099)	0.861 (0.165)	0.385 (0.143)	0.243 (0.207)	0.530 (0.136)
11	20	0.892 (0.120)	0.814 (0.169)	0.406 (0.118)	0.285 (0.185)	0.525 (0.110)
12	6	0.979 (0.047)	0.936 (0.122)	0.334 (0.198)	0.158 (0.220)	0.545 (0.199)
13	7	0.977 (0.051)	0.931 (0.127)	0.339 (0.194)	0.165 (0.221)	0.543 (0.193)

(.) notates a constant ψ or *P*; (ch) notates canopy height; (db) notates canopy dieback.

to *Prosopis* abundance: common duiker (*Sylvicapra grimmia*); springbok (*Antidorcus marsupialis*); Cape hare (*Lepus capensis*); African wildcat (*Felis silvestris lybica*); and an unidentified species of the *Muridae* family (Fig. 2a–e). The first three species showed a decline in occupancy with increasing *Prosopis* abundance: *S. grimmia, A. marupsialis* and *L. capensis* (Fig. 2a,b,e, respectively). On the other hand, the occupancies of *F. s. lybica* and the *Muridae* species were higher with increasing *Prosopis* abundance (Fig. 2c,d).

Discussion

This study aimed to assess how desert mammals that use riparian vegetation along ephemeral river beds might be affected by the invasive tree *Prosopis*. In the 1980s, a campaign was initiated and undertaken by park staff to physically remove all *Prosopis* from the eastern portion of the park (camera traps 10–13), and biological control was trialled near the west boundary of the park (camera traps 1 & 2). The camera traps recorded with low *Prosopis* density largely reflect the location of these activities. It is therefore reasonable to assume that observed wildlife distributions in this study reflect the abundance of *Prosopis.* Twenty-three species from eight mammalian Orders were detected in the riparian vegetation along the Swakop River in the dry austral winter of 2010, suggesting that a wide array of mammals utilize the riparian vegetation supported by the ephemeral river (Table 2). Camera traps are an increasingly popular technique for the noninvasive monitoring of wildlife, bringing numerous benefits such as accuracy in species identification and use in remote areas (Silveira, Jácomo & Diniz-Filho, 2003; Tobler *et al.*, 2008). Our systematic survey provides a recent assessment of mammals in this area and is therefore informative to private landowners, park managers and government and NGO officials throughout Namibia as well as being useful for future studies in this region.

The results from this study suggest that, in this ephemeral river system, *Prosopis* has no significant impact on mammal species richness (Fig. 1). At a global scale, invasive species clearly have a negative impact on biodiversity (Sax & Gaines, 2003), but at a local scale, there are mixed results concerning their negative, neutral or positive effects on wildlife (Mazzotti, Ostrenko & Smith, 1981; Garcia, Finch & Leon, 1998; Sax, 2002). In particular, previous studies have shown that total species richness can remain constant or vary only slightly in response to changes in vegetation composition and structure, despite the fact that the composition or abundance of species assemblages can drastically alter due to colonization and extinction events (Brown *et al.*, 2001; Parody, Cuthbert & Decker, 2001). Simply assessing how vegetation alterations affect species richness may therefore overlook how

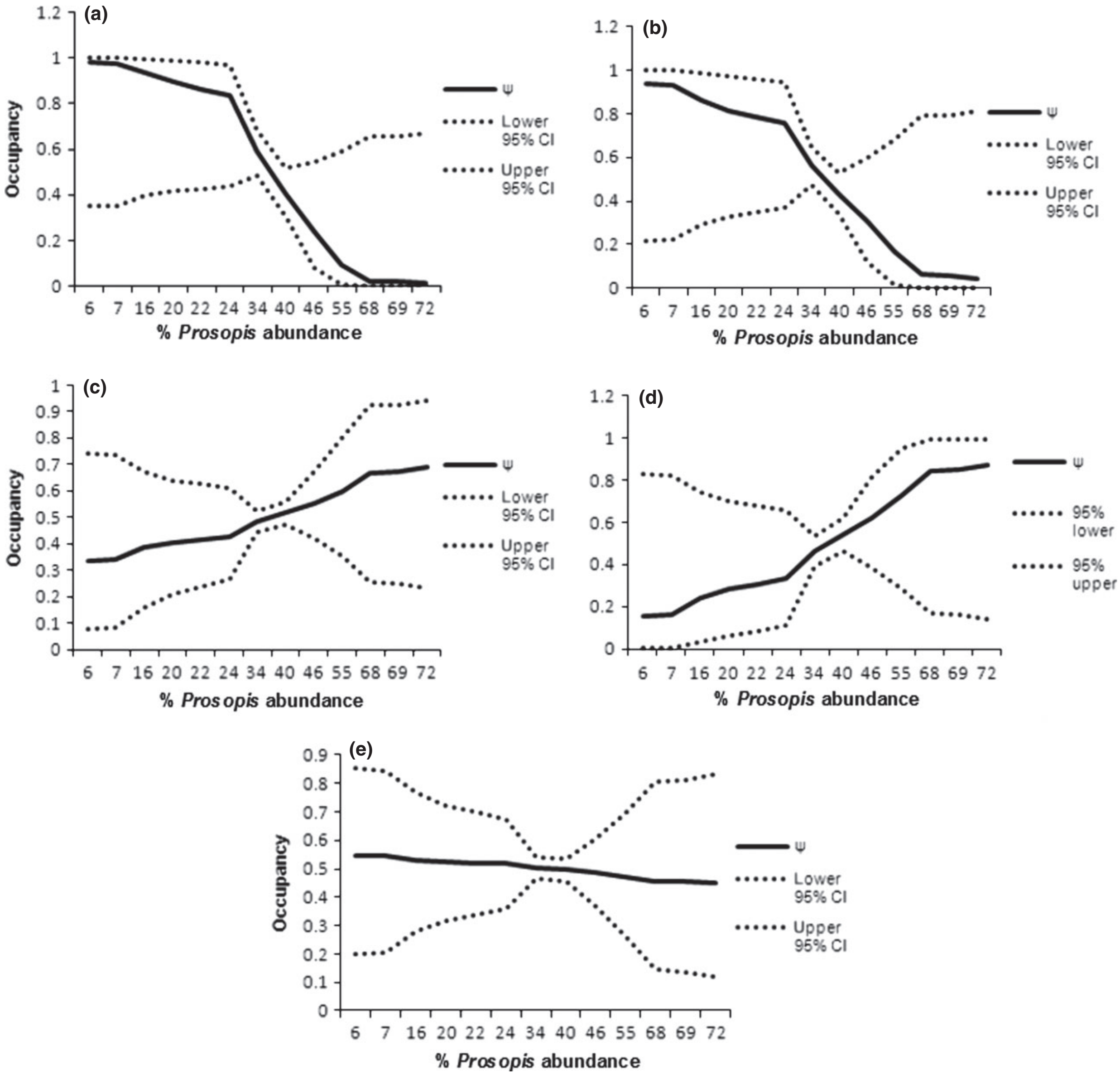

Fig 2 Profiles of variation in estimated occupancy for five mammals in the ephemeral Swakop River in the Namib-Naukluft National Park: (a) *S. grimmia*, (b) *A. marsupialis*, (c) *F. s. lybica*, (d) Muridae species and (e) *L. capensis*

particular species are affected. This may have detrimental implications for threatened species, particularly as it appears that there are species-specific responses in occupancy to *Prosopis* invasion.

The unidentified *Muridae* species showed the strongest positive response to *Prosopis* abundance (Fig. 2d). In areas where the tree is native, *Prosopis* pods and seeds constitute a significant part of small rodent diet (Pasiecznik *et al.*, 2001); therefore, small rodents in the Swakop River may benefit from *Prosopis* presence. A positive response, albeit less marked, was also described for the African wildcat, *F. s. lybica* (Fig. 2c). Although little is known about the ecology of small wild cats, evidence suggests that they are opportunistic hunters with a prey preference for small rodents (Herbst & Mills, 2010). It therefore seems possible that the positive response of the *Muridae* species to *Prosopis* abundance leads to a positive response in *F. s. lybica*. The fact that the response was more muted in the predator relative to prey is consistent with previous observations that the effects of invasive plants on native species can be dampened through trophic levels (Scherber *et al.*, 2010). In contrast, two ungulate species, the common duiker and the springbok (Fig. 2a,b), show a negative association with *Prosopis* abundance. This pattern is puzzling, not only because both are browsers and thus likely to forage on fallen *Prosopis* pods, but also because a third ungulate browser, the greater kudu, is unaffected by *Prosopis*. In this case, the reduced occupancy of the two smaller ungulates may reflect an increase in predation risk from leopards (as the low canopy heights of *Prosopis* may reduce visibility and the availability of escape routes for small ungulates) that does not affect the much larger kudu.

Carbone *et al.* (2001) found that 1000 camera trap days were sufficient to detect large cats at very low densities in dense forests, whilst 1035 camera trap days were sufficient for Silveira, Jácomo & Diniz-Filho (2003) to successfully investigate mammal abundance and richness in grassland habitat: our trapping effort should therefore be adequate for robust species inventory and species richness analyses. However, results show that numerous species were only detected once or twice: it is possible that the rarely caught species may be using the river merely as a transportation corridor, explaining their low detection probabilities. Because the camera traps were located in woodlands (as opposed to the open channel), the wildlife is most likely 'using' the habitat as opposed to pure locomotion. It has then been suggested that low detection probabilities can produce biased occupancy estimates (Mackenzie & Royle, 2005), explaining why reliable occupancy models could only be built for eight species. These results imply that a higher trapping effort should be considered in future work.

Ephemeral rivers are ecologically and economically important, and yet, these systems are especially vulnerable to invasion because their dynamic hydrology facilitates the movement of alien species (Hood & Naiman, 2000; Richardson *et al.*, 2007). *Prosopis* invasion is considered a critical threat to the riparian ecosystems of ephemeral rivers in southern Africa (Bethune, Griffin & Joubert, 2004; Joubert, 2009) and thus may pose a threat to the mammals that utilize these habitats. Whilst the results of this study show that no differences in species richness could be detected between areas of high or low *Prosopis* abundance and that there are species-specific responses to *Prosopis*, caution is advised when extrapolating these results. This is because we only sampled during one season (the dry austral winter) in one single year. Yet, in the wet season, wildlife usage of the river is thought to be less due to the wide availability of vegetation and water sources in the surrounding area. Due to highly variable precipitation (Mendelsohn *et al.*, 2009), wildlife movements may also vary between years. Therefore, future research would benefit from surveying over multiple seasons and years. We recommend future work also includes systematic observations on browse damage across tree species and other environmental factors, such as accessibility to the river bed, in order to develop a better understanding of mammal distributions in this region.

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