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Human population density explains alien species richness in protected areas

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ABSTRACT

Understanding the drivers of biological invasions, across taxa and regions, is important for designing appropriate management interventions. However there has been no work that has examined potential drivers of both plant and animal invasions, for both species considered to be aliens and those that are invasive. We use South Africa's national park system (19 national parks, throughout South Africa and covering ~39,000 km^2) as a model to test the generality of predictors of alien species richness in protected areas. We also compare the predictors of alien versus invasive species richness, and alien plant versus alien animal species richness. Species were classified as alien, invasive (having known negative impact on biodiversity) or extralimital, using standard definitions. Potential predictors (numbers of years since the park was proclaimed and since new land was acquired, park area, data availability, human population density in the vicinity of the park, number of roads, number of rivers, indigenous plant species richness and normalised difference vegetation index) of the number of alien and invasive species in national parks were examined for plants and animals using generalised linear models. Human population density surrounding parks was a significant and strong predictor of numbers of alien and invasive species across plants and animals. The role of other predictors, such as NDVI and park age, was inconsistent across models. Human population density has emerged here as an important predictor of alien species richness in protected areas across taxa, providing a basis for guidelines on where to focus surveillance and eradication efforts.

1. Introduction

Although protected areas remain a cornerstone of global biodiversity conservation strategies, with the intention of being afforded the highest level of protection, they remain susceptible to anthropogenic change. For example, options for ameliorating the effects of climate change in individual protected areas are limited and difficult to implement (Dawson et al., 2011). Habitat loss, by contrast, is generally less of a direct threat within protected area systems than it is outside (although see for example Bruner et al., 2001). Nonetheless, habitat change in the vicinity of protected areas, especially where human populations are expanding significantly (Wittemyer et al., 2008), has a broad range of consequences for conservation, many of which involve interactions between different forms of environmental change (McDonald et al., 2009). Human activities in the matrix fragment the landscape, further isolating protected areas and exacerbating their vulnerability to external influences. Importantly, increasingly degraded and invaded boundaries act as a propagule source, facilitating alien invasion of protected areas (Pyšek et al., 2002; Alston and Richardson, 2006; Foxcroft et al., 2011a). Indeed, alien species pose a substantial threat to biodiversity in many protected areas (e.g. Pyšek et al., 2002; Allen et al., 2009), and are commonly considered a management priority because of the threat that they pose to the ecological performance of these areas (Randall, 2011).

Nonetheless, biological invasion is one form of environmental change that can, at least to some extent, be successfully managed (Tu, 2009). Such management is critically dependent on adequate information and an understanding of the source, size and nature of invasion (McGeoch et al., 2010). This includes the identity, number and invasion status of alien species, as well as the drivers and pathways of alien species introductions (Kolar and Lodge, 2001). Further consideration must also be made for the phenomenon of lag phases in invasions, whereby a species can be resident in a novel locality for a substantial amount of time before becoming invasive; due to factors such as the availability of sites for invasion,

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biotic interactions and environmental conditions (see Richardson et al., 2011). Preventing invasion is by far the most efficient and cost-effective management option, particularly in protected areas (Tu, 2009). Understanding what drives introductions, the numbers of species that become invasive, and how this varies across taxonomic groups, therefore provides an essential basis for the formulation of appropriate policy and management approaches.

The drivers of alien species richness *per se*, versus invasive species, i.e. defined here as those species that impact negatively on biodiversity (see McGeoch et al., 2010), may also differ. A relatively small percentage of alien species are considered to be invasive (Richardson and Pyšek, 2006), and Richardson et al. (2005) found somewhat different predictors of numbers of alien versus invasive plant species richness across quarter degree grid cells (QDGCs) in South Africa (number of aliens was related more to human factors and invasive species richness was better predicted by environmental factors). As a consequence of generally inadequate information on the known or potential impacts of alien species on biodiversity (Vilà et al., 2010), and the characteristic lag effect associated with establishment and spread (Wonham and Pachepsky, 2006), the management of biological invasions must necessarily consider a broad suite of alien species, in addition to those known to have negative biodiversity impacts. As resources available for the management of biological invasions are virtually always inadequate, those species considered to pose the greatest threat to biodiversity need to be prioritized for management action via some form of risk assessment (Hayes, 1997; Hulme, 2011).

In addition to differences between alien and invasive species, alien plants and animals generally have different introduction pathways, as well as biodiversity impacts (Hulme et al., 2008; Vilà et al., 2010). Alien plant invasion of protected areas has most commonly been shown to be significantly related to human movement and density, as well as indigenous species richness (for example in the USA (McKinney, 2002), the Czech Republic (Pyšek et al., 2002) and South Africa (Macdonald et al., 1986)). By contrast, the roles of other environmental variables (such as climate), human factors (roads and various other disturbance effects) and protected area-specific characteristics (such as park age) are often comparatively less important and more variable across studies (see Appendix A). Few studies have examined predictors of alien animal invasion of protected areas and these studies have indicated that proximity to human settlements and human modified habitats are also particularly important (Smallwood, 1994; McKinney, 2006). Minimizing invasive species threats to protected areas must necessarily consider both plant and animal invasions, and the fact that alternative approaches may well be necessary for managing them (Tu, 2009).

Here we identify significant predictors of alien species richness using South Africa's national park system as a model. In addition to a sizeable and comparatively well known alien fauna and flora, South Africa has a rapidly growing human population, rich biodiversity and extensive protected area network. The South African National Parks (SANParks) estate covers about 39,000 km^2 (approximately the size of Taiwan), and as such provides one of the largest studies of protected area invasion of this kind (although see White and Houlahan (2007) on alien richness in Canadian protected areas). The country's 19 national parks constitute 52% of terrestrial protected area in the country, span the country geographically and encompass a diverse range of park sizes (from 57 to 19,624 km^2), urban to rural contexts, climates and biomes (SANParks, 2010). They therefore provide an ideal model system for examining predictors of biological invasion in protected areas. Furthermore, we test the generality of predictors of protected area invasion by determining whether these predictors are similar for alien species overall, versus that subset that has a negative biodiversity impact (i.e. invasive species). We also test whether these predictors are similar across and within taxonomic groups, specifically plants and animals.

2. Methods

2.1. Data compilation

The list of 813 alien species in South Africa's 19 national parks was used in this study (from Spear et al., 2011). Alien species were classified as being either extralimital, i.e. indigenous to South Africa but not indigenous to a particular park (Spear and Chown, 2008), and alien to South Africa, based on literature and database searches for information on the indigenous range of each species. Searches were conducted for information on biodiversity impacts of each species in its introduced range using Thomson Reuters Web of Science and Google Scholar. For each species we recorded whether the species is known to be invasive elsewhere in its introduced range as an indication of potential invasiveness here (following McGeoch et al., 2010; Hayes and Barry, 2008). The designation of species as invasive here therefore represents those species that have been demonstrated to be invasive locally, as well as those that are considered to have the potential to become invasive based on evidence of their invasiveness elsewhere.

Total counts per national park were made of the number of (1) alien, (2) extralimital and (3) invasive (i.e. demonstrated biodiversity impacts anywhere in the world) species per taxonomic class and kingdom. Spatial autocorrelation in the data was investigated using correlograms constructed (in SAM, http://www.ecoevol.ufg.br/sam/) for the species richness variables, with significance determined following Oden (1984). No significant spatial autocorrelation at $p < 0.05$ was found across the parks for any of these variables.

2.2. Predictors of numbers of alien species

Twelve variables were selected as potential predictors of the number of alien species per national park, including environmental variables, human activity variables and protected area characteristics: (1) number of years since the park was proclaimed (years), (2) number of years since the most recent land acquisition (years), (3) park size (km^2), (4) data availability (categorical estimates with three levels), (5) visitor numbers (mean annual), (6) boundary human population density (total population density in the vicinity of the park across the three boundary QDGC's with the highest population densities), (7) number of roads entering the park, (8) number of rivers entering the park, (9) indigenous plant species richness (per QDGC), (10) normalised difference vegetation index (NDVI), (11) mean annual temperature (°C) and (12) mean annual rainfall (mm). These variables were selected based on current understanding of the determinants of alien species richness, particularly for protected areas (Appendix A).

Variables (1) and (2) above were obtained from Park Management Plans (http://www.sanparks.org/conservation/park_man/approved_plans.php) and were used to determine the year that each national park was proclaimed and the most recent year (up to 2010) that new land was acquired for inclusion in each national park. In cases where parks were recently renamed or merged, the earliest or most realistic intermediate year of full protection for the area was used. (3) The area of national parks was obtained from the 2010 SANParks GIS boundary shapefile with 2011 updates. (4) When compiling lists and counting numbers of alien species the amount of available information must be considered because this may bias richness estimates (McGeoch et al., 2012). In this case, underestimates of the numbers of alien species present are likely for those national parks with less invested in surveys and research on alien species (McGeoch et al., 2010). Thus, before data were collated we scored each national park as being either data deficient, data intermediate or data rich for alien species information, based on expert knowledge (i.e. the authors familiar with the different parks, and the research conducted in them). We assumed that the estimates of numbers of invasive species per park would be more accurate than estimates of alien species because invasives are more likely to be noticed and are better known. (5) The mean number of tourists visiting each national park annually was calculated from five recent tourist seasons (2005/2006–2009/2010) from the SANParks annual reports (http://www.sanparks.org/about/annual/default.php). (6) Human population density per quarter degree grid cell (QDGC) in the vicinity of each national park was calculated using census data from Statistics South Africa (Statistics South Africa, 1996). The sum of the three boundary QDGC's with the highest human population densities were used to accommodate very high variability in population density across some parks, to deal with two parks bordering neighbouring countries where comparable estimates were not available (although population density is known to be low in these few cells), and to best represent invasion risk to each park. (7) and (8) ArcGIS 9.3 (ESRI, Redlands) was used to map South Africa's rivers (third order or greater) (CSIR, 2004), tar roads (http://www.mapcruzin.com/free-south-africa-arcgis-maps-shapefiles.htm) and SANPark's boundaries and then the number of rivers and tar roads entering each park was counted. (9) The estimate of indigenous plant species richness used was the mean number of indigenous plant species per QDGC for those cells encompassed by and overlapping with SANParks boundaries. This estimate was calculated using data extracted from The National Herbarium Pretoria Computerised Information System (PRECIS) (http://posa.sanbi.org/intro_precis.php), available at a QDGC scale (see also Richardson et al., 2005). (10) January and July normalised difference vegetation indices (NDVIs) (calculated from 1982 to 1999) were used as a measure of net primary productivity, and were obtained from the African Real Time Environmental Monitoring using the Meteorological Satellites Programme of the Food and Agriculture organisation. The mean of January and July NDVI was used. (11) and (12) Mean annual rainfall and mean annual temperature per national park were calculated from Schulze (1997). Continuous explanatory variables were $\log_{10}$ transformed prior to analysis to ensure linear contribution to the models.

Variables that influence alien species richness in parks have been shown in many cases to be significantly correlated amongst themselves (McKinney, 2002). The first step to resolving this problem was to use Spearman ranked correlations as an initial assessment of collinearity of predictor variables, and to exclude strongly correlated variables ($r_s > 0.60$). The most highly correlated parameters were 'mean annual rainfall' with 'NDVI' with (0.86) and boundary human population density (0.64); 'mean annual number of visitors' with 'boundary human population density' (0.75); and 'temperature' with 'number of rivers' (0.67). The 'visitor', 'rainfall' and 'temperature' variables were thus excluded from models *a priori*, resulting in nine predictors for consideration (Appendix B).

Best fit generalised linear models for the number of alien and invasive species were determined for (a) all species, (b) plants, (c) animals (all animal taxa, vertebrate and invertebrate), (d) vertebrates (including all mammals, birds, fish, reptiles and amphibians), and (e) mammals only (the species richness of the remaining taxa was too low for independent analysis). Models were fitted using a Poisson distribution and a negative binomial in cases with high overdispersion (Quinn and Keough, 2002). First, full models were run for the total number of alien species, and the data subsets using the nine selected predictors. The best model was taken as the model with the lowest AIC (Burnham and Anderson, 2002). These analyses were conducted for all of the different subsets of data, i.e. alien and invasive data for different taxonomic groupings. Models were run in R 2.15.1 (R Project Development Team, http://www.r-project.org/), using the MASS (Venables and Ripley, 2000) and bestglm (A.I. McLeod and C. Xu, 2011; http://cran.r-project.org/web/packages/bestglm/bestglm. pdf) libraries.

3. Results

3.1. Alien species diversity

A total of 1670 species by national park records were compiled, including 813 alien species (Spear et al., 2011), of which 181 were considered invasive (i.e. evidence of negative impact on biodiversity locally or elsewhere, see methods). The alien species burden is highly unevenly distributed across parks, more so for plants than animals (Fig. 1). The national parks with the most alien and invasive species were Kruger (400 and 81 species), Table Mountain (291, 101), Garden Route (200, 74) and Addo Elephant (130, 59) National Parks (NPs) (Fig. 1). The national parks with fewest recorded alien and invasive species were Kalahari Gemsbok (15, 7) and Richtersveld (14 and 12 species) National Parks (Fig. 1).

Most of the alien species (64.33%) were recorded in only a single national park (Fig. 2), and the majority of these were recorded in those parks with the most alien species overall (i.e. Kruger and Table Mountain National Parks). There were 76 extralimital species in total (23 animal [including 11 mammals, 6 fish, 2 birds, 2 insects, 1 reptile, 1 amphibian] and 53 plant species) (Fig. 3). Biocontrol agents constituted 4% and domestic and livestock animals a further 1% of the total number of alien species. One fifth of the alien plant species were considered invasive (20%), whereas over a third of the alien animal species were designated as invasive (31%) (Fig. 2). The invasive species that were recorded in most parks were also the most frequently recorded alien species, and included the house sparrow (*Passer domesticus*), feral cat (*Felis catus*), Brazilian tree tobacco (*Nicotiana glauca*) and sweet prickly pear (*Opuntia ficus-indica*) (Appendix D).

Alien plants made up the majority of alien species (81.55% of species and 82.51% of records) in national parks and all national parks had at least eight alien plants (Fig. 1). The plant families with the most species were Fabaceae (66 species), Poaceae (62) and Asteraceae (52). The animal groups with the most species in the 19 national parks were insects (44 species), mammals (26), gastropods (19), freshwater fish (16), springtails (11) and birds (9) (Fig. 1d, Appendix C). The majority of insects listed (30 of 44) were species deliberately introduced as biological control agents for management purposes (Fig. 3). Alien mammals included a number of feral, domestic and livestock species ($n = 7$), e.g. cats (*F. catus*) (16 NPs), dogs (*Canis familiaris*) (8 NPs), goats (*Capra hircus*) (9 NPs), cattle (*Bos taurus*) (6 NPs) and donkeys (*Equus asinus*) (4 NPs), and game hunting animals from surrounding properties, e.g. fallow deer (*Dama dama*) (4 NPs), impala (*Aepyceros melampus*) (3 NPs), nyala (*Tragelaphus angasii*) (3 NPs), wild boar (*Sus scrofa*) (2 NPs), waterbuck (*Kobus ellipsiprymnus*) (2 NPs) and springbok (*Antidorcas marsupialis*) (2 NPs) (Appendix D). Most of the game animals were extralimital rather than alien to South Africa (10 of 14). The large majority of alien birds included human commensal species (species benefiting from human habitation and food), e.g. house sparrow (*P. domesticus*) (16 NPs), feral pigeon (*Columba livia*) (12 NPs), European starling (*Sturnus vulgaris*) (9 NPs) and Indian myna (*Acridotheres tristis*) (4 NPs), as well as extralimital or range expanded species, e.g. hadeda ibis (*Bostrychia hagedash*) (7 NPs) and helmeted guineafowl (*Numida meleagris*) (7 NPs).

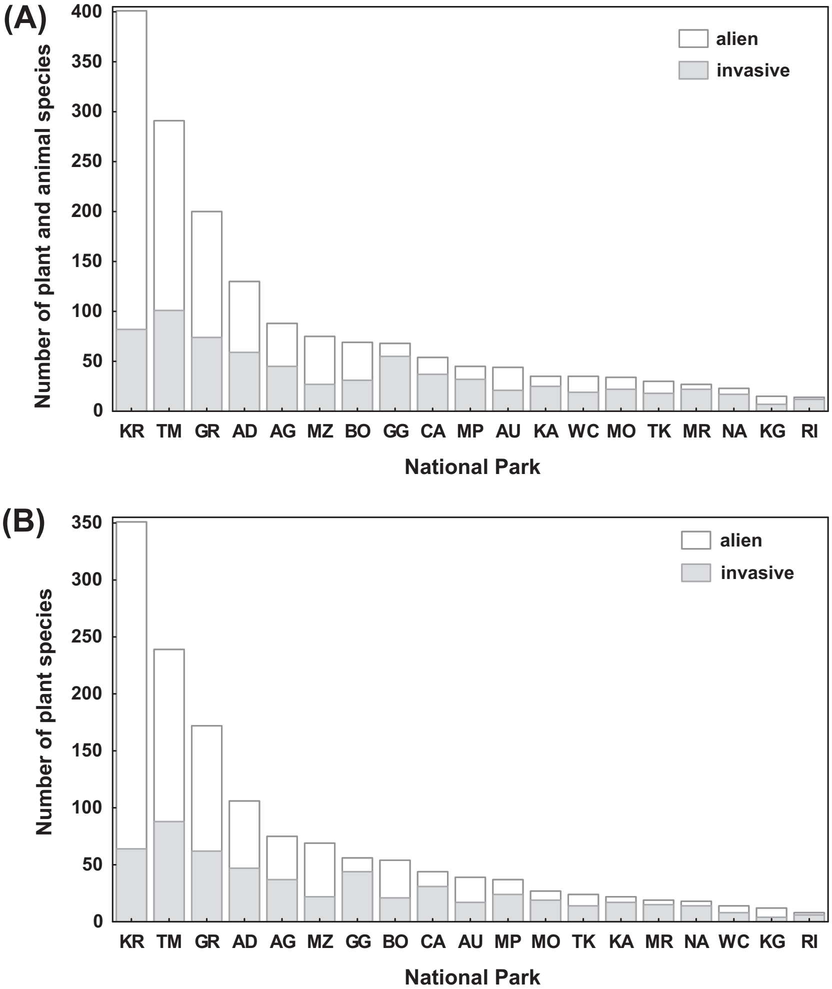

Fig. 1. Number of alien and invasive species per national park for (A) all species, (B) plants and (C) animals, as well as (D) the number of alien animals per park and per taxon. National parks (total number of species): AD: Addo Elephant (130), AG: Agulhas (88), AU: Augrabies Falls (88), BO: Bontebok (69), CA: Camdeboo (54), GR: Garden Route (200), GG: Golden Gate Highlands (68), KG: Kalahari Gemsbok (15), KA: Karoo (35), KR: Kruger (400), MP: Mapungubwe (45), MR: Marakele (27), MO: Mokala (28), MZ: Mountain Zebra (75), NA: Namaqua (23), RI: Richtersveld (14), TM: Table Mountain (291), TK: Tankwa Karoo (30) and WC: West Coast (35).

3.2. Predictors of the numbers of alien and invasive species per park

Nine of the 10 best-fit explanatory models were significant; the alien animal model was not significant (Table 1). The best fit models for all alien and invasive species together, versus alien and invasive plants on their own, were very similar (Table 1); a likely consequence of the dominance of plant over animal species richness (82% of species were plants). As a consequence, plant and animal models were considered separately. The deviance explained was high for both the plant and animal models (>70%), although slightly higher for alien (>76%) than for invasive species models (Table 1).

There were significantly more alien plants in parks with higher NDVI and higher surrounding human population density (Table 1). Data availability also played a significant role (Table 1). The model for invasive plants was similar, with the exception that invasive plant numbers tended to be higher in smaller parks and NDVI was not part of the best fit model (Table 1). The alien and invasive animal models differed from each other with older parks tending to have fewer alien but not invasive animals and data availability playing a significant role for alien but not invasive animals. However, parks with high surrounding human population density had both significantly more alien and invasive animal species (Table 1). The role of human population density surrounding parks was thus consistent across alien and invasive, and plant and animal models (Table 1). It was also the only and significant explanatory variable in the alien vertebrate and invasive mammal models, alone explaining 29% and 16% of the deviance in richness respectively (Table 1). The contribution of number of rivers, park age and size and indigenous plant richness were inconsistent across models, each in different and only single cases (Table 1). Years since land acquired and number of roads did not contribute to any best fit models.

4. Discussion

4.1. What drives numbers of alien species in protected areas?

Human population density surrounding parks was the most consistent predictor of numbers of alien and invasive species across both plants and animals. Although there were other significant explanatory variables and some interrelated ones (as observed elsewhere (McKinney, 2002) and here for example visitor numbers to the park and local human population density), two contrasting examples illustrate the overriding importance of human population numbers. The Kruger National Park (NP), which has the highest number of alien species, is the oldest park with about 110 years of continuous conservation status. Kruger NP is

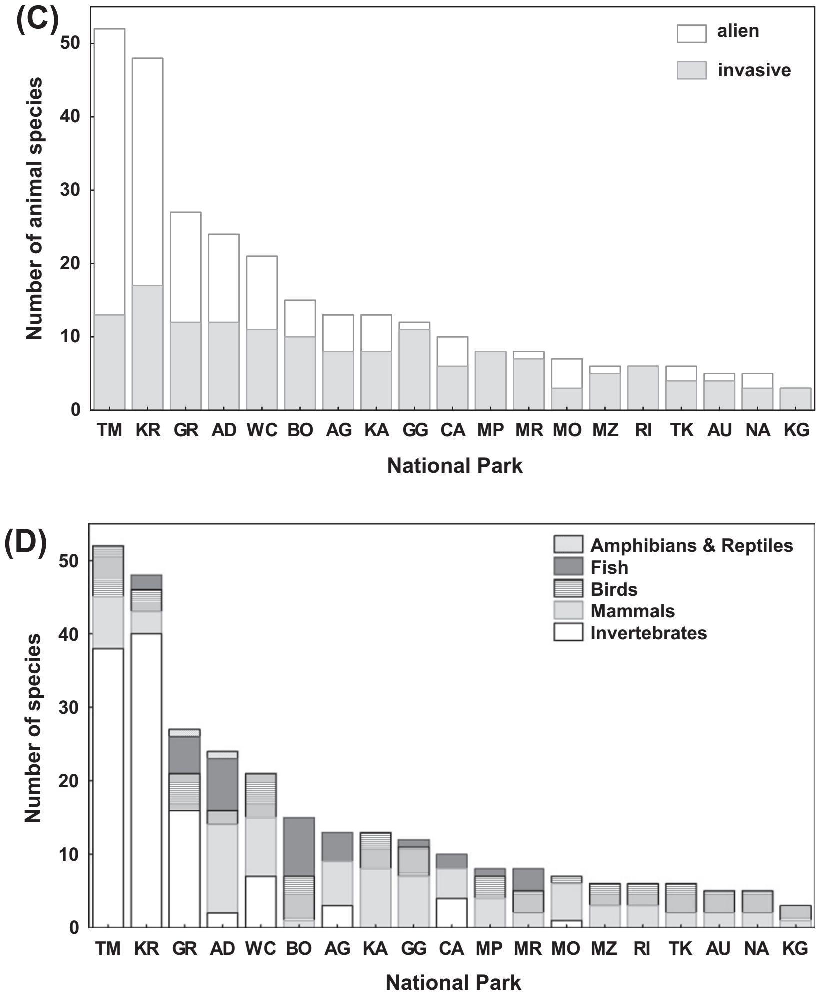

Fig. 1. (*continued*)

also found in a relatively arid savanna with about 530 mm rainfall per year. However, the human population surrounding Kruger can account for both the numbers of alien plants as well as invasive plants, as at least 2 million people reside within a 50 km radius of the park (Pollard et al., 2003), and more than 3600 staff members reside within the park (Foxcroft et al., 2008). The second highest number of alien species (also the highest number of invasive species) was found in Table Mountain NP, with a Mediterranean climate situated in the biodiverse Fynbos biome (Mucina and Rutherford, 2006). Different sections have been proclaimed since 1939, with the park only fully consolidated as recently as 1998. Table Mountain NP is an urban park, falling within the Cape Town metropolitan area, with a large surrounding human population (~3 million people) (Holmes et al., 2012). Although the southernmost and oldest section of the current park was proclaimed over 70 years ago, most other sections of the park have a history of use for a range of purposes that have inflated alien and invasive species numbers in the park, including plantation forestry. Therefore, although these two parks have very different histories and contexts, both are clearly impacted, at least in terms of alien species numbers, by the people living along their borders.

The second most consistently significant term in the explanatory models was data availability. This term was included because it was apparent *a priori* that historical survey effort for alien species differed to some extent across parks (Spear et al., 2011). Whereas invasive species, particularly animals, are likely to be highly conspicuous and therefore included in park alien species inventories, the presence of non-invasive alien species may be insidious, with a long lag between arrival and establishment in the park and discovery by park management; a situation not unique to protected areas (McGeoch et al., 2012). This is especially likely to be the case in larger, more remote and less densely staffed parks, such as Kalahari Gemsbok and Richtersveld NPs. This finding nonetheless re-affirms the importance of regular surveillance and effective monitoring of alien and invasive species in protected areas (Foxcroft and McGeoch, 2011; Tu, 2009).

The remaining significant predictors of alien richness varied across alien, invasive, plant and animal models. Drivers of invasion that are known to be important elsewhere (Appendix A), as well as for particular parks included in this study, were not generally significant across the suite of parks examined here. For example, rivers are known to be an important pathway for the spread of alien species, with transportation of alien propagules downstream and riverine areas favouring invasion due to the temporary availability of nutrients, high resource availability and disturbance (Stohlgren et al., 1998; Foxcroft et al., 2007; Richardson et al., 2007). While this is generally the case for protected areas when watersheds fall outside their boundaries and mitigation requires the cooperation of neighbouring landowners, it has also been specifically demonstrated for one of the parks

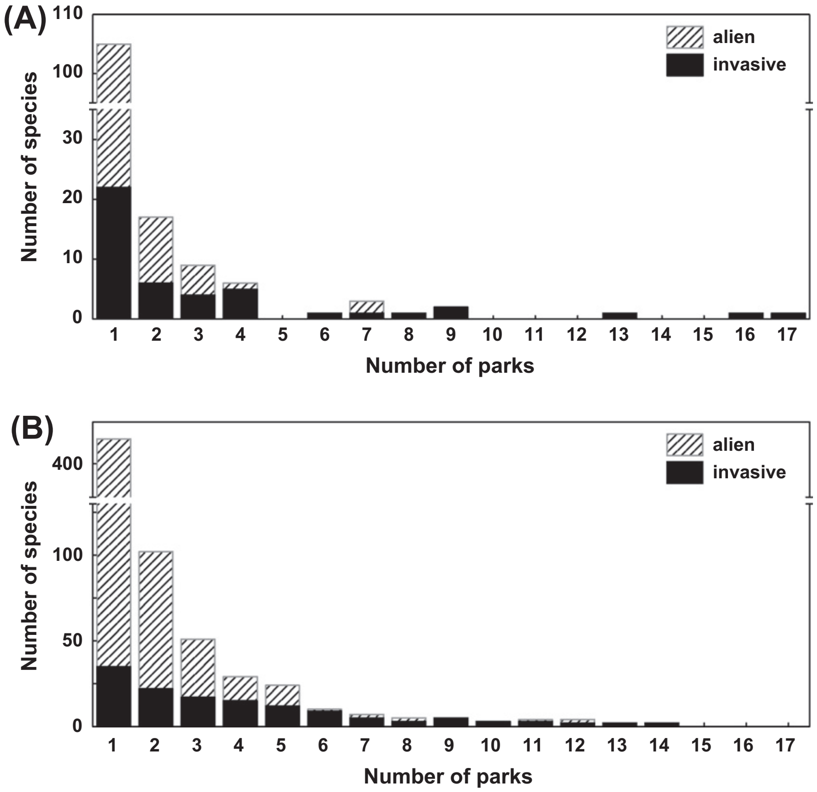

Fig. 2. Composite occupancy of alien and invasive alien species in national parks in South Africa, (A) animals and (B) plants.

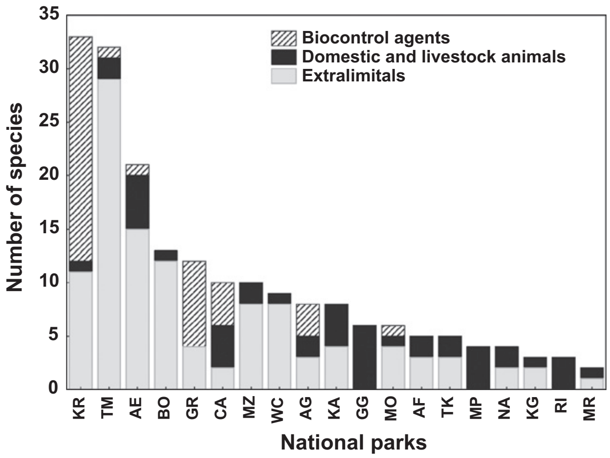

Fig. 3. Number of alien species in national parks in South Africa that are biocontrol agents, domestic and livestock animals and extralimital species.

in this study, i.e. the Kruger NP which has seven major rivers and has a combined drainage area of 52,169 km^2 (e.g. Foxcroft et al., 2007). Nonetheless, although rivers have been shown to be important pathways of introduction of alien species from extensive catchments upstream from the park boundaries in Kruger NP (Foxcroft et al., 2007), this does not necessarily reflect the invasiveness of the species introduced via this pathway, illustrating the often context dependence of drivers of biological invasion.

The higher number of alien animals found in more recently proclaimed parks is likely to be a legacy of previous land uses and other human associated disturbance (e.g. Pyšek et al., 2002). In general the more recently established and expanded national parks often encompass some areas that historically were subject to agriculture, human settlement and associated alien species introductions and subsequent invasion. Both Garden Route (SANParks, 2008) and Addo Elephant (SANParks, 2012) NPs have recently consolidated a large area, including pockets of a variety of other land-uses, such as plantation forestry and stock farming. While this legacy of alien invasion is perhaps an under-appreciated and unintended consequence of the otherwise generally positive current trend of significant protected area expansion in South Africa and elsewhere (Butchart et al., 2010), its effect was found to be significant only for alien animals in the park system examined here.

The many variables considered in protected area studies to date (Appendix A) include several correlated and also contradictory predictors of invasion, providing little clarity on the problem that can be generalised across species and systems. Our study, involving a diverse protected area system over a large area and considering multiple alien and invasive taxa supports this context dependence for several predictors. However, it does show that surrounding human population density provides a single and most consistently significant predictor of alien richness in parks. Human activity is well known to promote the introduction (as domestic pets, livestock and garden plants) (Hulme et al., 2008; Silva-Rodriguez and Sieving, 2012), establishment and persistence (through disturbance) of alien species (Hobbs and Huenneke, 1992). Species therefore enter protected areas aided by animal vectors and humans, as well as by natural diffusion from invaded areas adjacent to parks (see Foxcroft et al., 2011a; Smallwood, 1994). We suggest that against this template our results provide a robust and widely applicable predictor for alien species invasions into protected areas.

Table 1
Best fit model results of the relationships between numbers of alien and invasive species and the tested predictors using Generalized Linear Models (negative binomial and Poisson distributions). Estimates are presented for parameters retained in the best model (years since land acquired and number of roads did not contribute to any of the models).

	All species		Plants		Animals		Vertebrates		Mammals	
	Alien	Inv.	Alien	Inv.	Alien	Inv.	Alien	Inv.	Alien	Inv.
Age					−0.61[*]			0.50		
Data_R	0.82[**]	0.35[*]	0.83[*]	0.68[*]	1.18[***]					
Data_I	0.15	−0.06	0.06	−0.13	0.59[**]					
Area				−0.39[*]						
Pop	0.53[***]	0.34[***]	0.52[***]	0.51[***]	0.69[***]	0.38[***]	0.32[**]	0.19[#]		0.33[*]
Rivers									−0.18	
Indig		0.40[**]								
NDVI	1.77[*]	1.21[**]	1.99[*]			1.13				
Res. dev. (d.f.)	19.73 (14)	22.44 (13)	19.89 (14)	21.33 (14)	18.91 (14)	10.77 (16)	17.50 (17)	13.77 (16)	20.65 (17)	20.75 (17)
DE (%)	82.40	85.97	76.79	72.53	89.78	70.06	28.78	40.17	15.46	16.44
LogL (d.f.)	−86.75 (6)	−66.16 (7)	−85.88 (6)	−68.92 (6)	−49.98 (5)	−41.56 (3)	−50.93 (2)	−41.81 (2)	−43.92 (2)	−36.31 (2)
Model	NB	NB	NB	NB	P	P	NB	P	NB	P
P<	0.001	0.001	0.001	0.001	0.001	0.001	0.01	0.01	ns	0.05
AIC	257.24	149.74	284.73	154.48	107.90	85.58	100.70	86.76	80.98	66.63

Age – Number of years since park proclaimed, Data_R – Data availability – rich, Data_I – Data availability – intermediate, Pop – Surrounding human population density, Rivers – Number of rivers, Indig – Indigenous plant richness, NDVI – normalised difference vegetation index, no asterisk denotes non-significant variable retained in best model, Res. dev., Residual deviance, DE – Deviance explained, d.f. – degrees of freedom, LogL – Log-likelihood, Model – NB (negative binomial) or P (Poisson), AIC – Akaike Information Criterion.

[*] Significant at $P < 0.05$.

[**] Significant at $P < 0.01$.

[***] Significant at $P < 0.001$.

[#] Significant at $P = 0.09$.

4.2. Are predictors of alien and invasive species richness the same?

Other than the consistent influence of human population, the predictors for the alien and invasive species subsets were neither consistent nor strong, with several predictors not contributing significantly to explaining richness. Differences between alien and invasive plant richness predictors include the fact that parks with higher NDVI (strongly correlated with rainfall) had more alien plants, whereas smaller parks had higher invasive plant richness. Much of the field of invasion biology has investigated predictors of species' invasiveness, or an areas' susceptibility to being invaded (see Foxcroft et al., 2011b for a discussion). These include species attributes, the susceptibility of habitats to invasion and propagule pressure. Nonetheless, these results illustrate that the role of human population density in generally increasing propagule loads is significant not only for introducing alien species, but also potentially invasive species. With sustained and growing pressure on areas neighbouring parks this risk of both alien and invasive species introductions is thus likely to increase, with a range of other, context-specific predictors determining relative numbers of alien versus invasive species.

4.3. Are the predictors of numbers of alien plants and animals the same?

Although there is a global increase in invasion by both animals and plants (McGeoch et al., 2010), no detailed comparison of the predictors of species richness has been undertaken for these groups in protected areas. Some understanding of common predictors would guide resource allocation and priorities for preventing and controlling invasions in parks generally (Foxcroft et al., 2011b). However, the only predictor that was consistent across plant and animal groups was human population density in the vicinity of protected areas and, with the exception of data availability (significant for alien animals), the predictor sets for plants compared with vertebrates (and the invasive mammal subset) were different. In fact, several explanatory variables considered in previous studies for plants were not significant here and also appear to be inappropriate predictors of animal invasions. While the drivers of alien animal (including invertebrates) richness per park included deliberate introductions, close human–animal associations are largely responsible for the richness of the invasive and alien vertebrate animal species subset (the situation may well be different for invertebrates, which are understudied, (McGeoch et al., 2011)). An estimate of close to 50% of the known alien animals in national parks in South Africa were either deliberately introduced (such as biocontrol agents, introduced to aid alien plant management, and some extralimitals), or could conceivably be prevented from entering parks (e.g. several of the livestock species) (Spear et al., 2011).

5. Conclusions

We demonstrate that human population density adjacent to protected areas is the most significant and consistent predictor of alien and invasive species richness for plants and animals studied across diverse environments. The positive association between human population density around protected areas and alien species richness is clearly yet another fingerprint of human-induced environmental change. This is especially important as protected areas are increasingly being relied on for biodiversity conservation and associated benefits; indeed the 'cornerstone' of many conservation efforts (Gaston, 2008; Barber et al., 2012). High human population density surrounding protected areas has important implications. Protected areas situated within or adjacent to highly populated urban areas with high alien species richness will face continuous pressure from both invasions by new alien species, but importantly, propagule pressure to maintain the status of current invasions, thus impeding management efforts (Vardien et al., 2012). Areas where rapid urban expansion is encroaching on long established protected areas will bring with it new alien and potentially invasive species. However, understanding the relative importance of predictors, such as those found here, provides insights into where surveillance and rapid responses to contain and potentially eradicate alien species may be attempted (van Wilgen and Biggs, 2011; van Wilgen et al., 2012). Mitigation strategies should thus include creating buffer zones, increased surveillance and monitoring along park boundaries for alien species incursions, and ongoing collaboration with adjacent land owners to achieve effective area-wide alien species management.

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Appendix A

Predictors of numbers of alien species in protected areas across published studies (see Table A1).

Table A1
Predictors of numbers of alien species in protected areas across published studies. +, significant positive relationship, –, significant negative relationship, S, significant categorical predictor, n.s. not significant. NR, Nature reserve, PA, Protected Area.

Parameter	Taxa	Country	Samples, area	Finding	References
Duration of influence					
1. Age of protected area	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	–	Pyšek et al., 2003
	Plants (alien)	USA	77 PAs	n.s.	McKinney, 2002
2. Duration of settlement	Plants (alien)	USA	77 PAs	+	McKinney, 2002
General park characteristics					
1. Area of protected area	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	n.s.	Pyšek et al., 2002
	Plants (invasive)	Southern Africa	41 NRs	n.s.	Macdonald et al., 1986
	Plants (alien)	USA	216 parks	+	Allen et al., 2009
	Birds and mammals (alien)	California, USA	11 NRs, 3032 km^2	n.s.	Smallwood, 1994
	Plants (alien)	USA	77 PAs	+	McKinney, 2002
2. Park shape (perimeter to area ratio)	Plants (alien)	USA	77 PAs	n.s.	McKinney, 2002
	Plants (problem alien)	New Zealand	234 NRs	+	Timmins and Williams, 1991
Human activity (see also roads)					
1. Disturbance (clearings, human use, rubbish)	Plants (problem alien)	New Zealand	234 NRs	+	Timmins and Williams, 1991
(stock use)	Plants (problem alien)	New Zealand	234 NRs	–	Timmins and Williams, 1991
2. Surrounding disturbance (dist. from settlement)	Plants (invasive)	Southern Africa	41 NRs	n.s.	Macdonald et al., 1986
	Birds and mammals (alien)	USA	11 NRs, 3032 km^2	+(no stats)	Smallwood, 1994
(agric. and settlements)	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	+	Pyšek et al., 2002
(located in larger PA) (surrounding habitat, steam source habitat)	Plants (problem alien)	New Zealand	234 NRs	Significant	Timmins and Williams, 1991
3. Human population density surrounding park	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	+	Pyšek et al., 2002
	Plants (alien)	USA	77 PAs	+	McKinney, 2002
4. Number of human visitors	Plants (invasive)	Southern Africa	41 NRs	n.s.	Macdonald et al., 1986
	Plants (alien)	USA	77 PAs	+	McKinney, 2002
	Plants (alien)	USA	216 parks	+	Allen et al., 2009
Climate and productivity					
1. Climate	Plants (alien)	USA	216 parks	n.s.	Allen et al., 2009
(Temperature and rainfall)	Plants (alien)	USA	77 parks	n.s.	McKinney, 2002
Temperature group (Temp., June isoth., rain.)	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	+, alt. out: –	Pyšek et al., 2002
(Rainfall)	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	n.s.	Pyšek et al., 2002
	Plants (invasive)	Southern Africa	41 NRs	Significant	Macdonald et al., 1986
2. Latitude	Plants (alien)	USA	216 parks	n.s.	Allen et al., 2009
3. Soil fertility	Plants (problem alien)	New Zealand	234 NRs	n.s.	Timmins and Williams, 1991
4. Range in elevation	Plants (alien)	USA	216 parks	+	Allen et al., 2009
Native diversity/habitat					
1. Phytogeographical region	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	n.s.	Pyšek et al., 2002
2. Vegetation type	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	n.s.	Pyšek et al., 2002
3. Scrubiness (% scrub and forest)	Plants (problem aliens)	New Zealand	234 NRs	+	Timmins and Williams, 1991
4. Biome	Plants, reptile and mammals	Southern Africa	41 NRs	n.s.	Macdonald et al., 1986
	Birds (invasive)	Southern Africa	41 NRs	Significant	Macdonald et al., 1986
5. Native species richness	Birds (alien and invasive)	Canada	42 NPs, 267,073 km^2	+	White and Houlahan, 2007

Table A1 (*continued*)

Parameter	Taxa	Country	Samples, area	Finding	References
	Birds and mammals (alien)	California, USA	11 NRs 3032 km^2	–	Smallwood, 1994
	Mammals (alien and invasive)	Canada	42 NPs, 267,073 km^2	–	White and Houlahan, 2007
	Plants (alien)	USA	216 parks	+	Allen et al., 2009
	Plants (alien)	USA	77 PAs	+	McKinney, 2002
	Plants (alien)	Czech Republic	302 NRs, 36.5 km^2	+	Pyšek et al., 2002
	Plants (alien and invasive)	Canada	29 NPs	+	White and Houlahan, 2007
	Plants (invasive)	Southern Africa and USA	41 and 21 NRs	+	Macdonald et al., 1989
	Plants (alien)	USA	216 parks	+	Allen et al., 2009
Pathways: Roads and rivers					
(proximity to road/rail)	Plants (problem alien)	New Zealand	234 NRs	–	Timmins and Williams, 1991
(road length)	Plants (alien)	USA	77 PAs	n.s.	McKinney, 2002
(trail coverage)	Plants (alien)	USA	216 parks	+	Allen et al., 2009
(river length)	Plants (alien)	USA	216 parks	–	Allen et al., 2009
(influent rivers)	Plants (invasive)	Southern Africa	41 NRs	n.s.	Macdonald et al., 1986

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Appendix B

Spearman correlation coefficients between continuous predictor variables (see Table B1).

Table B1
Spearman correlation coefficients <0.60 between continuous predictor variables retained for modelling.

	Age	Land	Area	Pop	Roads	Rivers	Indig	NDVI
Age	1.0	0.49*	0.32	0.36	0.45	0.28	0.18	−0.02
Land		1.0	0.29	−0.04	0.15	0.30	−0.28	−0.29
Area			1.0	−0.07	−0.01	0.42	−0.35	−0.22
Pop				1.0	0.53*	−0.26	0.49*	0.54*
Roads					1.0	−0.28	0.06	0.25
Rivers						1.0	−0.11	−0.19
Indig							1.0	0.35
NDVI								1.0

Age – Number of years since park proclaimed, Land – Number of years since most recent land acquisition, Area – Park size, Pop – Surrounding human population density, Roads – Number of roads, Rivers – Number of rivers, Indig – indigenous plant richness, NDVI – normalised difference vegetation index.

* Significant at $P < 0.05$.

Appendix C

Alien species per taxonomic group (see Table C1).

Table C1
Summary of alien (and the subset of invasive alien) species in South Africa's national parks by taxonomic group, species per group and number of national parks that each taxonomic group occurs in.

Group	No. of species	No. of invasives	No. of Parks	Group	No. of species	No. of invasives	No. of Parks
Plants	663	135	19	Arachnids	3	1	1
Insects	44	6	6	Bivalves	2	2	3
Mammals	26	13	18	Fungi	2	0	2
Freshwater fish	16	9	9	Millipedes	2	0	1
Gastropods	19	6	4	Amphibians	1	0	1
Birds	9	5	17	Reptiles	1	0	1
Springtails	11	1	3	Sea anemones	1	0	1
Earthworms	4	0	1	Centipedes	1	0	1
Ascidians	3	1	2	Barnacles	1	1	1
Soft shelled crustaceans	3	0	1	Bacteria	1	1	1

Appendix D

Species recorded in the most parks, as well as birds, domestic, livestock and game species (see Table D1).

Table D1
Alien and invasive species recorded in the most parks, as well as birds, domestic, livestock and game animals.

Species	Vernacular	Family	Number of parks
Most widespread species			
Passer domesticus[*]	House sparrow	Passeridae	17
Felis catus[*]	Feral cat	Felidae	16
Nicotiana glauca[*]	Brazilian tree tobacco	Solanaceae	14
Opuntia ficus-indica[*]	Sweet prickly pear	Cactaceae	14
Columba livia[*]	Feral pigeon	Columbidae	13
Datura stramonium[*]	Thorn apple	Solanaceae	13
Ricinus communis[*]	Castor oil plant	Euphorbiaceae	13
Arundo donax[*]	Giant reed	Poaceae	12
Pennisetum setaceum[*]	Fountain grass	Poaceae	12
Argemone ochroleuca	Sweet mexican poppy	Papaveraceae	12
Eucalyptus globulus	Blue gum	Myrtaceae	12
Lantana camara[*]	Lantana	Verbenaceae	11
Datura ferox[*]	Large thorn apple	Solanaceae	11
Cereus jamacaru[*]	Queen of the night	Cactaceae	11
Cirsium vulgare[*]	Scotch thistle	Asteraceae	11
Agave sisalana	Sisal	Agavaceae	11
Schinus molle[*]	Peruvian pepper	Anacardiaceae	10
Salsola kali[*]	Russian thistle	Amaranthaceae	10
Bird species			
Passer domesticus[*]	House sparrow	Passeridae	17
Columba livia[*]	Feral pigeon	Columbidae	13
Sturnus vulgaris[*]	European starling	Sturnidae	9
Bostrychia hagedash	Hadeda ibis	Threskiornithidae	7
Numida meleagris	Helmeted guineafowl	Numididae	7
Acridotheres tristis[*]	Indian myna	Sturnidae	4
Anas platyrhynchos[*]	Mallard	Anatidae	4
Gallus gallus	Chicken	Phasianidae	1
Domestic and livestock species			
Felis catus[*]	Feral cat	Felidae	16
Capra hircus[*]	Goat	Bovidae	9
Canis familiaris[*]	Dog	Canidae	8
Bos taurus[*]	Cattle	Bovidae	6
Equus asinus[*]	Donkey	Equidae	4
Equus caballus	Horse	Equidae	1
Gallus gallus	Chicken	Phasianidae	1
Ovis aries[*]	Sheep	Bovidae	1
Game animals			
Dama dama[*]	Fallow deer	Cervidae	4
Damaliscus pygargus[E]	Bontebok	Bovidae	4
Aepyceros melampus[E]	Impala	Bovidae	3
Tragelaphus angasii[E]	Nyala	Bovidae	3
Antidorcas marsupialis[E]	Springbok	Bovidae	2
Connochaetes taurinus[E]	Blue wildebeest	Bovidae	2
Kobus ellipsiprymnus[E]	Waterbuck	Bovidae	2
Sus scrofa[*]	Feral pig	Suidae	2
Equus burchellii[E]	Plain’s zebra	Equidae	1
Hemitragus jemlahicus[*]	Himalayan tahr	Bovidae	1
Hippotragus niger[E]	Sable	Bovidae	1
Oryx gazella[E]	Gemsbok	Bovidae	1
Phacochoerus africanus[E]	Warthog	Suidae	1
Tragelaphus strepsiceros[E]	Greater kudu	Bovidae	1

[*] Invasive somewhere.
[E] Extralimital.

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