South Africa's private wildlife ranches protect globally significant populations of wild ungulates

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Abstract

Reversing biodiversity loss is a global imperative that requires setting aside sufficient space for species. In South Africa, an estimated area of 20 million hectares is under wildlife ranching, a form of private land enterprise that adopts wildlife-based land uses for commercial gain. This land has potential to contribute towards biodiversity conservation, but the extent to which this occurs has not been evaluated. Using structured questionnaires of 226 wildlife ranchers, we assessed how the sector contributes towards the conservation of ungulates and elephants (hereafter herbivores). Overall, 40 herbivore species were present across the sample, where individual ranches had a mean of 15.0 (±4.8) species, 1.9 (±1.5) threatened species, and 3.6 (±3.1) extralimital species per property. In comparison to 54 state PAs, wildlife ranches had significantly higher species richness, more threatened species but more extralimital species when property/reserve size was controlled for. Ranches conducting trophy hunting had similar species richness and numbers of extralimital species per ha, but fewer threatened species when compared to ranches conducting ecotourism. We estimate that 4.66–7.25 million herbivores occur on ranches nationally, representing one of the few examples on earth where indigenous mammal populations are thriving and demonstrating how sustainable use can lead to rewilding. We discuss the potential negative impacts of widespread game fencing on landscape fragmentation and gene flow,

as well as how the widespread occurrence of extralimital species may lead to hybridisation, biotic homogenisation, and changes to vegetation dynamics. Despite these challenges, commercial wildlife ranching offers a viable option for conserving large mammalian herbivore biodiversity.

Keywords

Wildlife ranches, Ungulates, Species richness, Metabolic biomass, Extralimital species, Fences

Declarations

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Consent to participate: Participants were contacted via telephone to request participation. They were provided with a verbal explanation of the purpose of the study and were told that their contributions would be confidential and anonymous. All data were aggregated for analysis and no personal information is divulged.

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1. Introduction

The earth is facing a sixth mass extinction, with over 1 million species now at risk of disappearing forever (IPBES 2019). The global present-day biomass of wild land mammals is thought to have declined sevenfold since pre-human times (Bar-On et al. 2018), while the geographic ranges of almost half the mammal species for which distribution data are available have undergone a range shrinkage of >80% within historic times (Ceballos et al. 2017). Large wild herbivores continue to undergo dramatic population declines and range contractions, particularly in developing countries (Ripple et al. 2015).

Although Africa retains an unparalleled diversity of ungulates, widespread declines have been recorded both inside and outside protected areas (PAs) across much of the continent (Norton-Griffiths 2000, 2007; Craigie et al. 2010; Ogutu et al. 2016; Lindsey et al 2017). Across much of the Savannah Biome, which is particularly important for ungulates, ungulate biomass is now dominated by livestock, while indigenous ungulates contribute <10% of the standing crop (Du Toit and Cumming 1999; Hempson et al. 2017). The region that has fared best is southern Africa (Craigie et al. 2010), although even there a substantial proportion of PAs are significantly depleted (Lindsey et al. 2017).

To reverse population declines, wild mammals will need greater access to space and suitable habitat to meet their ecological requirements. This has traditionally been attempted through the expansion of state-owned PAs (Gallo et al. 2009; Craigie et al. 2010) and was formalised through the Convention on Biological Diversity (CBD). Aichi Target 11 of the CBD urged nations to, amongst other things, conserve at least 17 % of terrestrial areas through PAs and other effective area-based conservation measures by 2020 (Secretariat of the Convention on Biological Diversity 2014) but, while there has been some success in reaching this target globally (Gannon et al. 2019), many countries have either not met the total area requirement or have not protected the right land to optimise biodiversity conservation (Maxwell et al. 2020). In Africa, some countries do not have additional land to set aside for expanding PAs while others face economic pressures that preclude the necessary levels of state investment in conservation (Lindsey et al. 2018).

The declaration of private protected areas (PPAs) provides a partial solution to the challenge of how to expand PA coverage while ensuring sufficient resourcing for effective management (De Vos et al. 2019; Shumba et al. 2020), and there is growing evidence that such areas have effectively conserved some features of biodiversity (Gallo et al. 2009; Shumba et al. 2020), including large mammalian herbivores (Clements et al. 2018). However, formal declaration requires strict management criteria that, in some cases, limits the ability of private landowners to be commercially viable. While state PAs are generally subsidised, albeit often insufficiently (Lindsey et al. 2018), conservation on private land typically needs to pay for itself, and if it is unprofitable, landowners may adapt business models to less ecologically friendly practices or abandon wildlife-based land uses (WBLU) altogether (Clements et al. 2016).

An alternative, market-oriented approach to private land conservation is the commercial use of wildlife on land not declared as PPAs, where the primary goal of keeping wildlife is often profit, but where conservation gains may be an outcome. Commercial WBLUs are widely practiced in South Africa, Namibia and Zimbabwe, and to a lesser extent Botswana, Mozambique and Zambia, where legislation has to varying extents provided private landowners with user rights over wildlife (Bond et al. 2004; Child 2009; Lindsey et al 2013a,b).

Over the last 50 years, the South African wildlife ranching sector has grown substantially, mostly through the conversion of marginal land previously used for livestock production, and now encompasses an area of 17–20.5 million hectares (National Agricultural Marketing Council unpublished report; Taylor et al. unpublished report). This is equivalent to 14–17% of the country's land surface area and is larger than the ~10% coverage achieved by the formal South African PA network (Department of Environmental Affairs 2019). Although most wildlife ranches do not officially contribute to the expansion of formal PAs as prescribed by Aichi Target 11, they do set aside land for wildlife and may instead make a meaningful contribution to Aichi Target 7, which calls for sustainable management of areas under agriculture to ensure conservation of biodiversity (Secretariat of the Convention on Biological Diversity 2014). They may also qualify as other effective area-based conservation measures under Aichi Target 11 that aim to achieve effective conservation outside of PAs.

While there is considerable evidence for financial and social sustainability of wildlife ranching on marginal land (Musengezi 2010; Muir et al. 2011; Van der Merwe et al. 2014; Cloete et al. 2015; Clements et al. 2016; Chiyangwa 2018; Saayman et al. 2018; Taylor et al. 2020), the biodiversity conservation impacts remain comparatively unknown (Taylor et al. 2020) and contested (Pitman et al. 2017). To assess one aspect of the biodiversity conservation impact of wildlife ranching, we examined occurrence and abundance data for ungulates (Artiodactyla and Perissodactyla) and African Elephants (*Loxodonta africana*) (hereafter referred to as 'herbivores') on private land in South Africa.

There have been unpublished reports of substantial increases in herbivore numbers on private land in South Africa, resulting from the expansion of wildlife ranching (du Toit 2007), but these have not been formally quantified. Using data derived from questionnaire surveys of private landowners, we assessed the extent to which the wildlife ranching sector has contributed towards the conservation of herbivores in South Africa by estimating species richness and animal numbers and comparing these estimates to those of state PAs. We consider the potentially negative outcomes of profit-oriented management by assessing the extent of fencing and the prevalence of extralimital species. The extent of fencing has conservation implications because fences fragment the landscape and reduce ecological connectivity (Boone and Hobbs 2004; Woodroffe et al. 2014), obstruct dispersal and migration of terrestrial mammals (Hayward and Kerley 2009; Kerley and Landman 2010; Child et al. 2019), impede gene flow (Hayward and Kerley 2009), and may have detrimental effects on rangeland condition if stocking rates are too high (Du Toit and Cumming 1999; Kerley and Landman 2010). Extralimital species may bring risks for native species such as resource competition, hybridisation, homogenisation, and changes to vegetation dynamics (Castley et al. 2001; Spear and Chown 2009a). We also make recommendations on steps that could be taken to build on the benefits of wildlife ranching while reducing its potential negative outcomes.

2. Methods

2.1. Property sampling

Properties were sampled as per Taylor et al. (2020). In brief, we surveyed 276 private commercial wildlife properties between September 2014 and January 2017 using face-to-face (n=124), telephonic (n=140) and email (n=12) interviews. Of the 276 surveys, 226 provided species data and 182 provided useable herbivore count data (Figure 1).

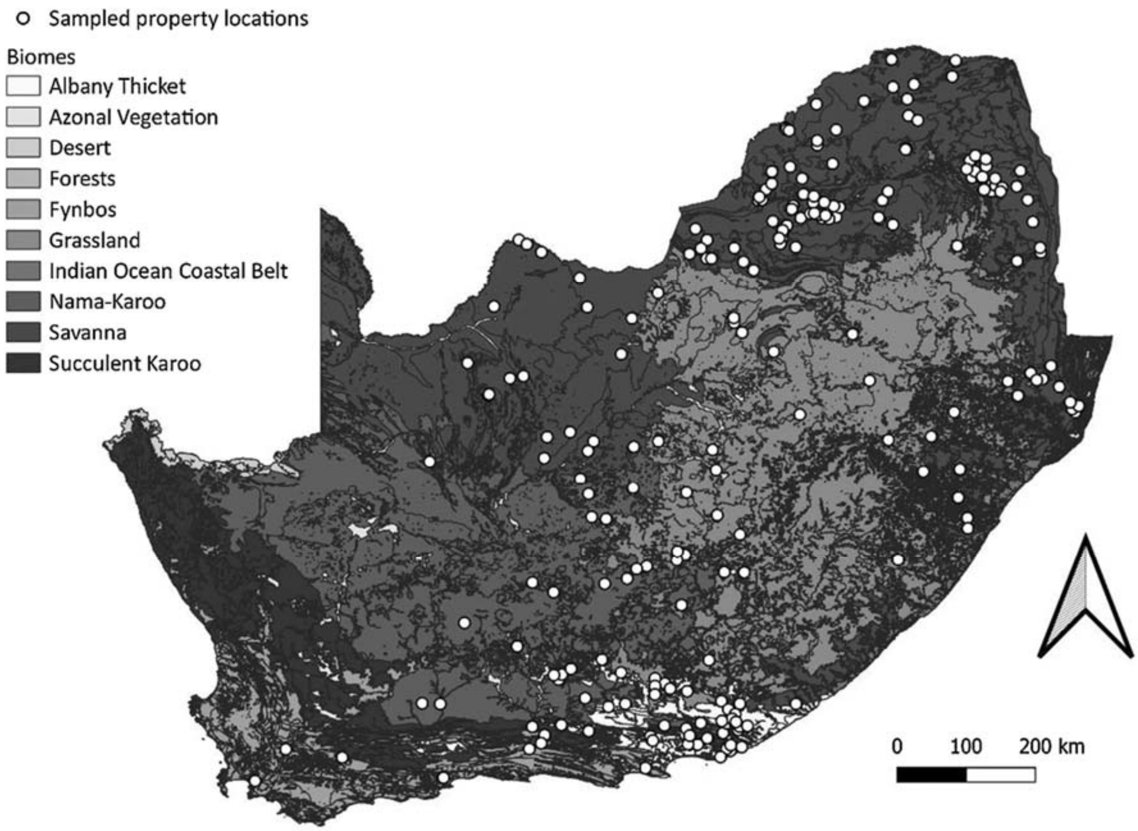

Fig. 1 Locations of 226 surveyed private wildlife properties across South Africa

2.2. Survey questionnaire

We obtained all the data for our analyses using a structured, pre-tested questionnaire of private landowners or managers. This was the same questionnaire used in Taylor *et al*. (2020), which was based on similar research assessing WBLUs in Namibia and Zambia (Lindsey et al., 2013b, 2013a). The questions relevant to this paper can be found in the online resources 1.

2.3. Property variables used in analyses

For each property we obtained the following information:

1) GPS location at entrance or property office.
2) Total property size, excluding intensive breeding camps, which are defined as small to medium-sized fenced enclosures in which animals are confined, protected from predators, and provided with most of their food, water, and veterinary requirements. Although camps tend to be small (e.g., 10–100 ha), there is no set definition for standard camp size; rather intensity of management interventions is more relevant (defined in online resources 2).

3) Type of perimeter fencing present (defined in online resources 2).

4) Dominant habitat type. To identify this, we intersected property GPS coordinates with vegetation layers (South African National Biodiversity Institute 2006) using QGIS (QGIS Development Team (2017), QGIS Geographic Information System, Open Source Geospatial Foundation Project. http://qgis.osgeo.org). Although most properties have multiple habitat types, we only considered the habitat at the GPS location to simplify analysis. We separated habitats by biome, but further separated the Savannah Biome into bioregions because most properties occurred in Savannah. For the remaining biomes, property sample size was too small to subdivide into bioregions.

5) Herbivore species richness. Participants were asked to indicate which wild herbivore species were present on their properties using a checklist to ensure that no species were missed. Species included were all the Artiodactyla, Perissodactyla and Proboscidea. Because 46% of surveyed properties had some level of intensive breeding (Taylor et al. 2020), which in many cases involved species held under higher than average densities, we differentiated species in breeding camps and extensive areas and only species data from extensive areas were included here. We defined extensive areas as those where wildlife moves freely on a property within the borders of the perimeter fence and with minimal human interference. See online resources 3 and 4 for species information and property-related data.

6) The number of extralimital species. These were defined as species occurring outside their natural historic distribution ranges (Birss et al. 2015), which may include species native to South Africa but occurring outside their historic range. We determined whether species occurring on each property were extralimital by intersecting the property GPS coordinates with the natural distribution range maps of Birss et al. (2015), which delineate the inferred natural distribution range of large mammals during the 500-year period ending in 1930. These maps do not include any of the small antelope species (duiker spp. (Family: Cephalophinae), grysbok spp. (Genus: *Raphicerus*), klipspringer *Oreotragus oreotragus*, oribi *Ourebia ourebi*, steenbok *Raphicerus campestris*, suni *Neotragus moschatus*) or pig species (bushpig *Potamochoerus larvatus* and warthog *Phacochoerus africanus*), so these were not included in the estimates. Non-native species (namely lechwe *Kobus leche* and deer species) were counted as extralimital.

7) Number of animals of each herbivore species. We excluded estimates from properties that did not conduct formal counts using drive or aerial methods (Bothma 2010), or which had not conducted a count within two years prior to the survey. We note that all herbivore counting methods carry some level of uncertainty

due to counting error (Peel and Bothma 1995; Redfern et al. 2002; Bothma 2010). While it is generally considered better to use repeatable, precise counting methods over a few years to monitor population trends (Bothma 2010), here we were interested in actual numbers. Because each property is different, counting biases would have been different for each property, so we did not attempt to estimate the level of error for each property. Rather than potentially introducing additional error through applying a correction, we used the numbers provided to us without any correction. Counting methods for most species tend to undercount animals (Peel and Bothma 1995; Redfern et al. 2002; Bothma 2010), so we likely underestimated actual numbers. We also excluded the following species from our count estimates because they are not generally counted due to characteristics like small body size or preferential selection of thick vegetation: bushbuck *Tragelaphus sylvaticus*, bushpig, duiker spp., grysbok spp., klipspringer, oribi, steenbok, suni, and warthog. Although kudu *Tragelaphus strepsiceros* are also difficult to count accurately, we included them due to their financial importance. See online resources 4 for property-related species data.

8) Large stock unit (LSU) equivalents of grazers and mixed feeders, calculated for each species using equation 1.

Equation 1:

$$LSU\ equivalent\ (species\ x) = \frac{Metabolic\ biomass\ (species\ x)}{Metabolic\ biomass\ of\ 450kg\ beef\ steer}$$

Where:

$$Metabolic\ biomass\ (species\ x) = number\ of\ animals\ (species\ x)\ \times unit\ mass\ (species\ x)^{0.75}$$

The unit mass of a species was calculated as the average mass of animals in a population of a species accounting for the fact that a population includes adult males, females, and young animals of varying ages (Cumming and Cumming 2003). We assumed an adult sex ratio of 1:1 and estimated the unit mass by multiplying the mean adult body mass of both sexes by 0.75 to account for juveniles (Taylor et al. 2020). Average species body masses for adult males and females were obtained from Bothma, van Rooyen and du Toit (2010) (see online resources 3).

The metabolic biomass of a 450kg beef steer is equivalent to 98 kg ($450^{0.75}$). Although larger animals have larger overall energy requirements, the mass specific metabolic demands of mammals tend to decline with increasing species size, with the energy requirements of herbivores having an allometric scaling exponent (slope) of ~0.75 (Müller et al. 2013).

Feeding guilds (grazers, browsers, and mixed feeders) of ungulates were assigned according to Bothma, van Rooyen and du Toit (2010) (see online resources 3) but we excluded browsers because there are no recognised methods for measuring browsing capacity.

9) The grazing capacity of each property. Estimated by intersecting property GPS coordinates against a spatial layer of national agricultural grazing capacity (Department of Agriculture, Forestry and Fisheries 2016). The long-term grazing capacity layer is a reference for the average LSU / ha a given landscape can sustainably support.

10) Type of dietary supplement provision.

2.4. Total number of wild herbivores on wildlife ranches in South Africa

We estimated the total number of animals across the entire wildlife ranching sector in South Africa by multiplying the median number per hectare by the total area of ranches. To account for the uncertainty around counting methods, we calculated 95% Confidence Intervals (CI) for the sample median using equation 2:

Equation 2:

$$\frac{n}{2} \pm \frac{1.96\sqrt{n}}{2}$$

where n = sample size. When the properties were sorted according to ascending order of animal densities, the lower and upper 95% CI values calculated using equation 1 corresponded with the properties with animal densities at the lower and upper 95% CIs. We used two estimates for total ranch area: 17 million hectares (Taylor et al. unpublished report) and 20.5 million hectares (National Agricultural Marketing Council unpublished report).

2.5. Comparison with national and provincial protected areas

Herbivore species richness estimates were obtained for 54 state PAs, while count data were only available for 12 state PAs. Data sources were national parks reports (South African National Parks 2012), provincial scientific services, and a database of species occurrence held by the Endangered Wildlife Trust. Species data were not available for PAs in all biomes and bioregions. Kruger National Park was included as two bioregions (Savannah Lowveld and Savannah Mopane).

2.6. Data analysis

Graphing and statistical analyses were conducted using R (v 3.5.1), while maps were produced using QGIS. We assessed whether species richness, number of threatened species, and number of extralimital species differed between wildlife ranches and PAs and whether they were affected by WBLU types (specifically ecotourism vs. trophy hunting). For species richness and number of threatened species, we conducted multiple regression analyses using the log link function for Poisson regression because the response variables were counts. The predictor variables included property type (wildlife ranch vs PA, with ranches being set as the baseline) and WBLU (set up as factors including ecotourism, trophy hunting, ecotourism plus trophy hunting, and neither activity, with ecotourism being set as the baseline), as well as three property-linked control variables we thought might influence species richness. These were: 1) log property size; 2) biome; and 3) whether a property was a mixed farm or wildlife only. Variables for biome and mixed farms were converted into factors, and the habitat with the highest average species richness (Albany Thicket) was used as the baseline against which the other habitats were compared. For statistical analysis of extralimital species, we followed the same procedure as for species richness, but used Quasi-Poisson regression because the response variable was over-dispersed.

3. Results

3.1. Average property size and fence configuration

The total extensive area covered by the original 226 surveyed properties, excluding breeding camps, was 1,138,365 ha. The median property size was 2,202 ha (IQ Range: 930–4627), varying from a median of 1,125 ha in Central Bushveld Savannah to 4,765 ha in the Nama-Karoo (Table 1). Based on 206 responses to fencing questions, 2% of properties had no fences, 13% had cattle fences and 85% had game fencing (of which 67% were stranded and 18% were Bonnox® fences). Overall, 43% had electrification around the perimeter, and 18% had electrical trip wires.

Table 1. Property sizes of 226 surveyed properties in nine habitat types

Biome (and Bioregion)	Count	Median (ha)	1st Quantile (ha)	3rd Quantile (ha)	Max (ha)
Albany Thicket	30	3,315	1,384	8,750	29,000
Fynbos	10	1,674	895	3,356	5,400
Grassland	31	2,000	999	3,700	10,000
Nama-Karoo	23	4,765	2,750	7,800	23,000
Savannah (Central Bushveld)	67	1,125	565	2,287	35,050
Savannah (Eastern Kalahari)	19	3,477	990	4,625	100,000
Savannah (Lowveld)	31	2,450	1,150	5,600	18,000
Savannah (Lowveld)	8	2,888	2,238	7,346	33,000
Savannah (Sub-Escarpment)	7	3,000	1,012	4,500	7,500

3.2. Species occurrence

A total of 40 wild herbivore species occurred on the 226 surveyed properties, of which two (Lechwe and Fallow Deer *Dama dama*) are not native to South Africa (Table 2). The most widespread species were common duiker *Sylvicapra grimmia*, kudu, impala *Aepyceros melampus*, warthog and steenbok, each occurring on >80% of properties. The least common species were oribi and suni, which occurred on <5% of properties. Out of the megaherbivores, giraffes *Giraffa camelopardalis*, were most common at 59% occurrence, followed by white rhinoceros *Ceratotherium simum* at 16%, African elephants at 14%, and black rhinoceros *Diceros bicornis* at 6%. Six species are listed as threatened (and three Near Threatened) on the global IUCN Red List of Threatened Species, while nine are threatened (and three Near Threatened) on the regional list (Child et al. 2016) (Table 2). Species occurrence distribution maps for which there are historic distributions are provided in online resources 5.

Table 2 Species occurrence, species numbers and IUCN Red List categories of large wild herbivores on surveyed properties.

Species	Number of properties	% occur.	Total count on surveyed properties (number of individuals)	Regional IUCN Red List	Global IUCN Red List
Common duiker	218	96.5	NA	LC	LC
Kudu	210	92.9	25,458	LC	LC
Impala	190	84.1	58,447	LC	LC
Warthog	186	82.3	NA	LC	LC
Steenbok	184	81.4	NA	LC	LC
Plains zebra	180	79.6	11,939	LC	LC
Waterbuck	159	70.4	7,388	LC	LC
Bushpig	150	66.4	NA	LC	LC
Blue wildebeest	149	65.9	18,682	LC	LC
Eland	143	63.3	9,175	LC	LC
Bushbuck	138	61.1	NA	LC	LC
Nyala	138	61.1	11,589	LC	LC
Giraffe	134	59.3	3,378	LC	VU
Blesbok	130	57.5	10,716	LC	LC
Red hartebeest	119	52.7	8,011	LC	LC
Gemsbok	116	51.3	12,943	LC	LC
Springbok	110	48.7	20,849	LC	LC
Mountain reedbuck	109	48.2	4,178	EN	EN
Klipspringer	75	33.2	NA	LC	LC
Common reedbuck	64	28.3	1,463	LC	LC
Buffalo	59	26.1	4,755	LC	LC
Black wildebeest	49	21.7	2,831	LC	LC
Hippo	45	19.9	NA	LC	VU
Sable	41	18.1	510	VU	LC
White rhino	36	15.9	NA	NT	NT
African elephant	32	14.2	1,059	LC	VU
Tsessebe	31	13.7	440	VU	LC
Rhebok	23	10.2	167	NT	NT
Blue duiker	21	9.3	NA	VU	LC
Cape grysbok	21	9.3	NA	LC	LC
Deer spp.	18	7.9	NA	Exotic	LC
Red duiker	17	7.5	NA	NT	LC
Roan	17	7.5	97	EN	LC
Bontebok	14	6.2	345	VU	NT
Lechwe spp.	14	6.2	NA	Exotic	LC
Black rhino	14	6.2	NA	EN	CR
Cape mountain zebra	14	6.2	511	LC	VU
Sharpe's grysbok	13	5.8	NA	LC	LC
Oribi	9	4.0	NA	EN	LC
Suni	8	3.5	NA	EN	LC

3.3. Species richness

The mean number of species on wildlife ranches was 15.0 (±4.8) (median = 15) (n=226) compared to 16.7 (±5.3) (n=54) on selected state PAs (median = 16) (Figure 2). After controlling for property size and biome, state PAs had significantly fewer (11% fewer) species than private land (Table 3). Species richness increased significantly with property size, while properties in Fynbos and Nama-Karoo had significantly fewer (29% and 26% fewer) species than Albany Thicket, which had the highest mean species richness (Figure 2 and Table 3). Properties in Savannah regions had intermediate numbers of species but did not differ significantly from Albany Thicket. Mixed farms had significantly fewer (12% fewer) species than wildlife only properties, but there was no significant difference between species richness on properties conducting ecotourism and properties conducting trophy hunting, although properties conducting both activities had significantly more species (17% more) than properties conducting neither activity (Table 3).

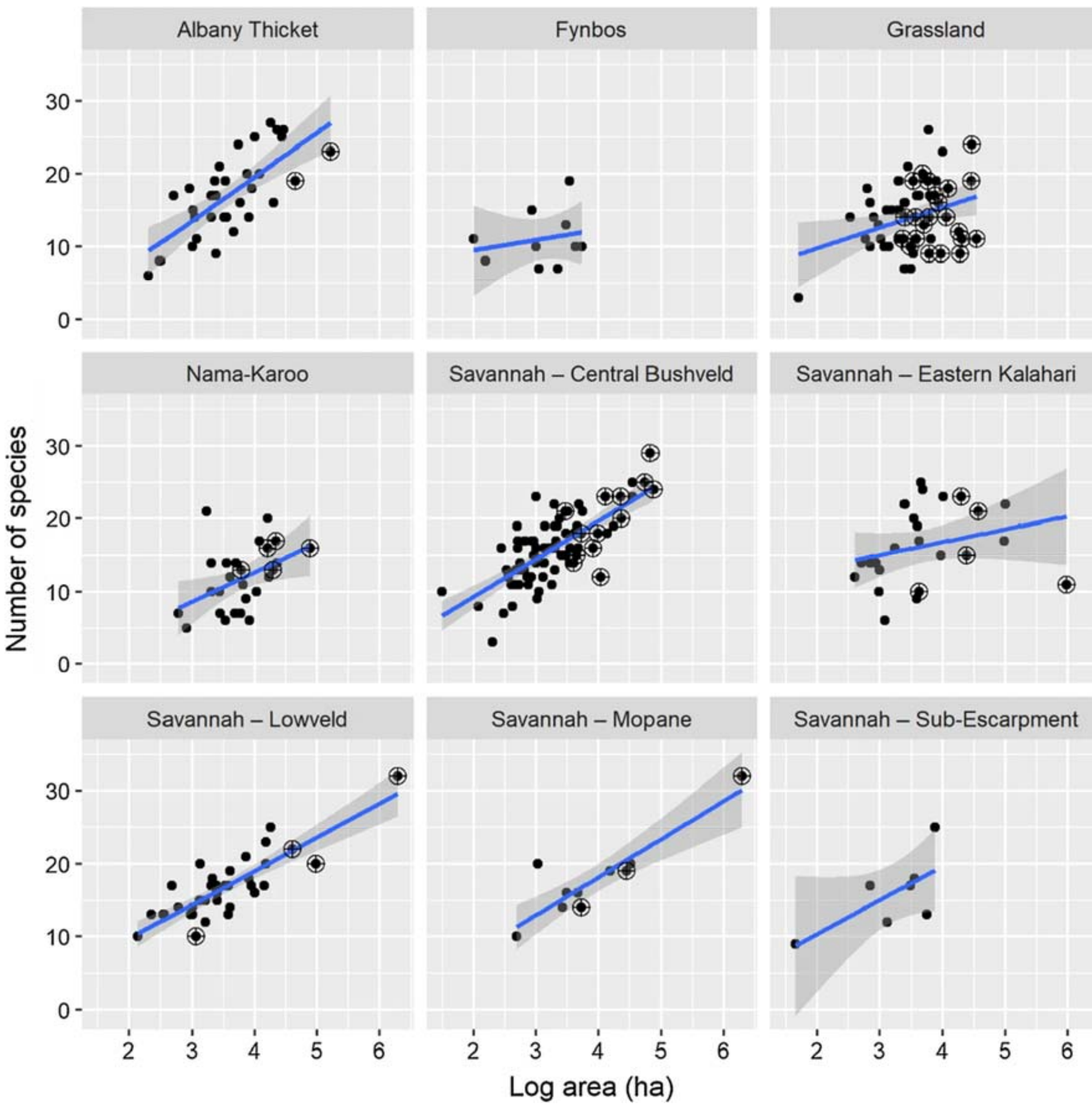

Fig. 2 Large herbivore species richness on 226 sampled wildlife ranches and 54 state PAs across nine habitat types. Note the x-axis represents the $\log_{10}$ of the area in ha. Black dots represent individual properties; circle/plus symbols represent state PAs in corresponding habitats

Table 3 Poisson model results for species richness on 226 surveyed private properties and 54 state PAs. Four of the five predictor variables (property type, mixed farming, habitat and WBLU activity) were included as factors. For property type, wildlife ranches were used as the baseline, while for mixed status, wildlife only properties were used as the baseline. For habitat, mean species richness was estimated before the regression analysis was conducted, and the habitat with the highest richness (Albany Thicket) was used as the baseline against which the other habitats were compared. For WBLU activities, ecotourism was used as the baseline to allow direct comparison with trophy hunting.

Full model equation:

Species richness ~ property type + log property size + biome + mixed status + WBLU

Results for selected model	Estimate	Std. error	P-value
Intercept	1.806	0.115	**<0.001**
Property type	-0.116	0.058	**0.045**
Log property area	0.266	0.028	**<0.001**
Biome–Sav. E Kalahari	-0.094	0.067	0.157
Biome–Sav Lowveld	-0.027	0.060	0.646
Biome–Sav Mopane	-0.105	0.086	0.222
Biome–Sav Sub-escarp	-0.004	0.105	0.971
Biome–Sav Central Bush	0.026	0.053	0.628
Biome–Grassland	-0.106	0.060	0.081
Biome–Nama-Karoo	-0.346	0.072	**<0.001**
Biome–Fynbos	-0.306	0.107	**0.004**
Mixed	-0.129	0.040	**0.001**
WBLU–Neither	-0.080	0.060	0.185
WBLU–Trophy	0.035	0.049	0.480
WBLU–Both	0.156	0.046	**<0.001**

3.4. Number of threatened species

The mean number of threatened species on wildlife ranches was 1.9 (±1.5) (median = 1) (n=226) compared to 2.6 (±1.9) (n=54) on selected state PAs (median = 2) (Figure 3). After controlling for property size and biome, state PAs had significantly fewer threatened species (35% fewer) than private land (Table 4). The number of threatened species increased significantly with property size, but there were no differences between biomes. Mixed farms had significantly fewer (30% fewer) species than wildlife only properties, while properties conducting trophy hunting had 25% fewer threatened species than properties conducting ecotourism only (Table 4).

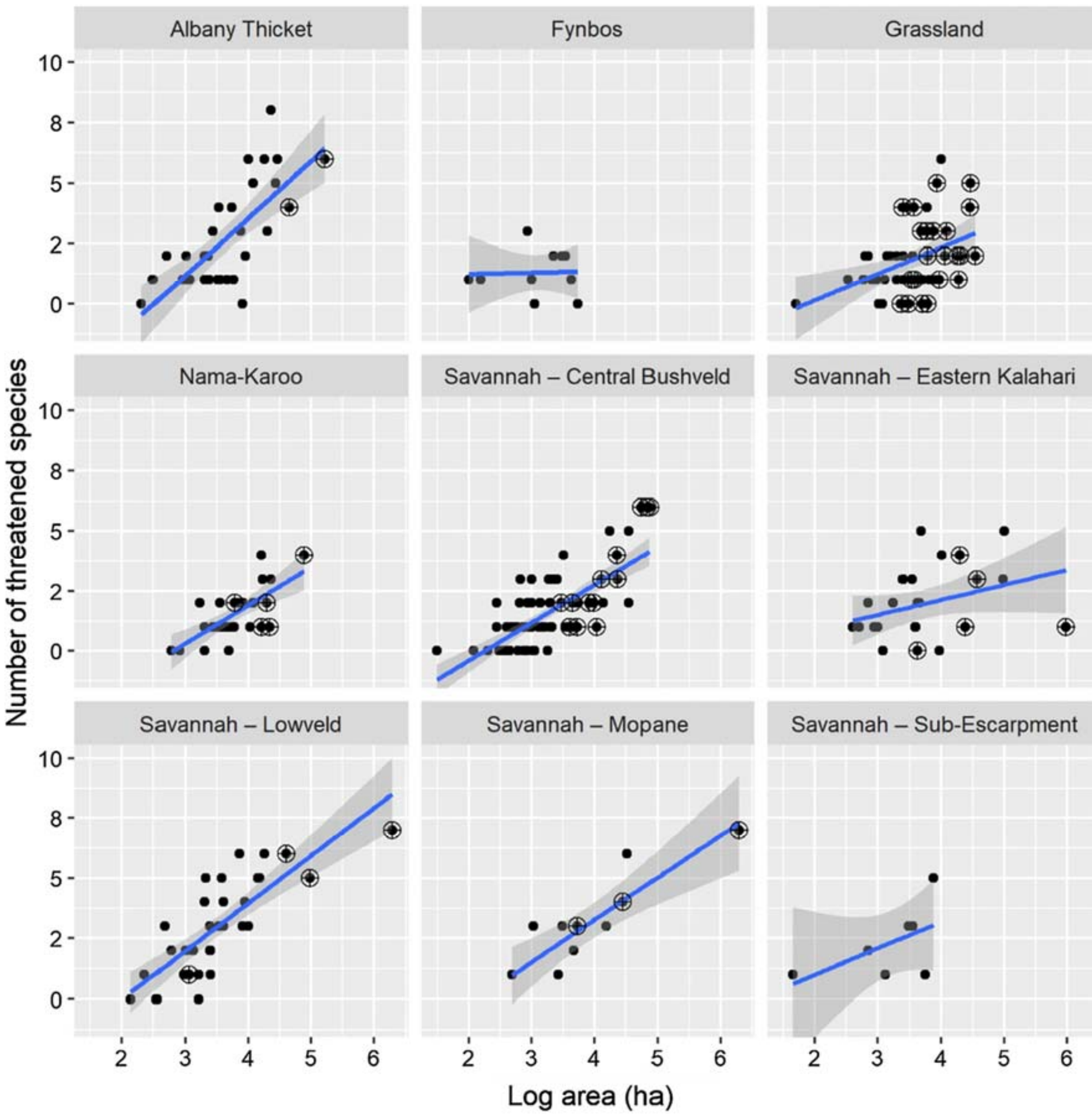

Fig. 3 Number of threatened large herbivore species on 226 wildlife ranches and 54 states PAs across nine habitat types. Note the x-axis represents the $\log_{10}$ of the area in ha. Black dots represent individual extensive properties; circle/plus symbols represent state PAs in corresponding habitats

Table 4 Poisson model results for the number of threatened species on 226 surveyed private properties and 54 state PAs. Four of the five predictor variables (property type, mixed farming, habitat and WBLU activity) were included as factors. For property type, wildlife ranches were used as the baseline, while for mixed status, wildlife only properties were used as the baseline. For habitat, mean species richness was estimated before the regression analysis was conducted, and the habitat with the highest number of threatened species (Savanna Mopane) was used as the baseline against which the other habitats were compared. For WBLU activities, ecotourism was used as the baseline to allow direct comparison with trophy hunting.

Full model equation:			
Number threatened spp.	~ property type + log property size + biome + mixed status + WBLU		
Results for selected model	**Estimate**	**Std. error**	**P-value**
Intercept	-1.463	0.350	**<0.001**
Property type	-0.433	0.153	**0.005**
Log property area	0.659	0.071	**<0.001**
Biome–Sav Lowveld	0.246	0.204	0.228
Biome–Albany Thicket	0.170	0.209	0.418
Biome–Sav Sub-escarp	0.188	0.315	0.550
Biome–Sav E Kalahari	-0.264	0.227	0.246
Biome– Grassland	0.098	0.214	0.646
Biome– Sav Central Bush	-0.048	0.204	0.812
Biome–Nama-Karoo	-0.243	0.238	0.307
Biome–Fynbos	-0.254	0.342	0.457
Mixed	-0.350	0.118	**0.003**
WBLU–Neither	0.229	0.180	0.205
WBLU–Trophy	-0.293	0.145	**0.043**
WBLU–Both	0.108	0.122	0.372

3.5. Extralimital species and overlapping congeners

Across all surveyed properties, 85% (n=191/226) had at least one extralimital species, while the mean and maximum number were 3.6 (±3.1) and 14 respectively (median=3) (Figure 4). The most frequent extralimital species were, in descending order, impala, nyala *Tragelaphus angasii*, blesbok *Damaliscus pygargus phillipsi*, waterbuck *Kobus ellipsiprymnus*, gemsbok *Oryx gazelle*, sable *Hippotragus niger*, giraffe, plains zebra *Equus quagga* and blue wildebeest *Connochaetes taurinus*. Among the state PAs included for comparison, 81% (n=44/54) had at least one extralimital species, while the mean and maximum number were 2.3 (±1.9) and 7, respectively (median=2) (Figure 4). With regards to exotic species, 8% (n=19/226) of wildlife ranches had lechwe and 9% (n=20/226) had deer species, while four state PAs had deer species.

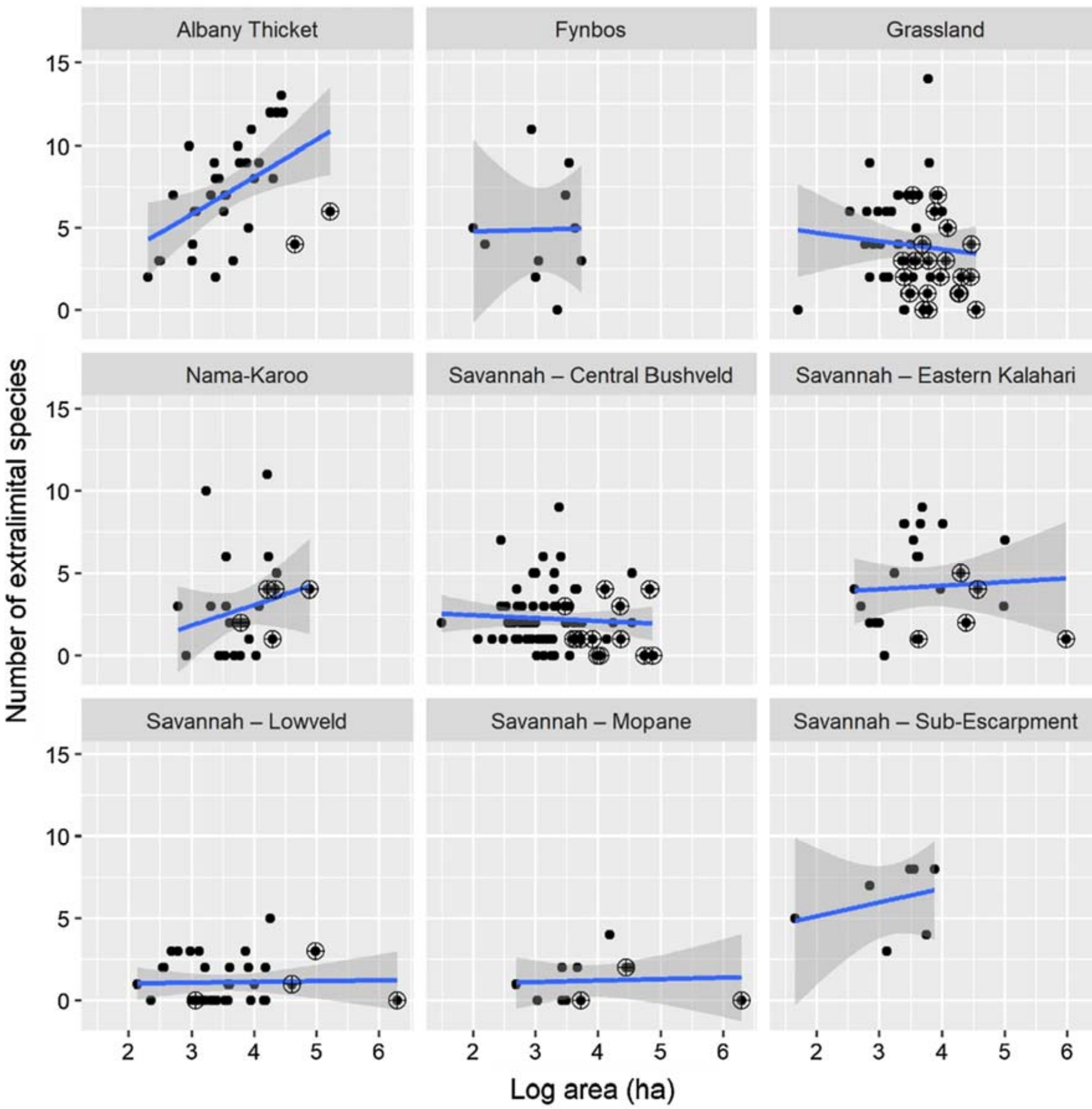

Fig 4 Number of extralimital large herbivore species on 226 wildlife ranches and 54 state PAs across nine habitat types. Note the x-axis represents the $\log_{10}$ of the area in ha. Black dots represent individual extensive properties; circle/plus symbols represent state PAs in corresponding habitats

The number of extralimital species increased with property size, while properties in Albany Thicket had significantly more extralimital species than properties in Grassland (28% more), Nama-Karoo (55% more) and most Savannah habitats (41–85% more) (Table 4). State PAs had significantly fewer (47% fewer) extralimital species than wildlife ranches, while there was no difference between the frequency of extralimital species on ecotourism properties and trophy hunting properties.

Table 5 Quasi-Poisson model results for extralimital species on 226 surveyed properties and 54 state PAs. Four of the five predictor variables (property type, mixed farming, habitat and WBLU activity) were included as factors. For property type, wildlife ranches were used as the baseline, while for mixed status, wildlife only properties were used as the baseline. For habitat, the mean number of extralimital species was estimated before the regression analysis was conducted, and the habitat with the highest number (Albany Thicket) was used as the baseline against which the other habitats were compared. For WBLU activities, ecotourism was used as the baseline to allow direct comparison with trophy hunting.

Full model equation:			
Number of extralimitals	~ property type + log property size + biome + mixed status + WBLU		
Results for selected model	**Estimate**	**Std. error**	**P-value**
Intercept	1.285	0.289	**<0.001**
Property type	-0.636	0.164	**<0.001**
Log property area	0.192	0.075	**0.011**
Biome–Sav Sub-escarp	-0.156	0.201	0.439
Biome–Fynbos	-0.308	0.196	0.117
Biome–Grassland	-0.335	0.126	**0.008**
Biome–Sav E Kalahari	-0.524	0.144	**<0.001**
Biome–Nama-Karoo	-0.799	0.164	**<0.001**
Biome–Sav Central Bush	-1.038	0.123	**<0.001**
Biome–Sav Mopane	-1.863	0.343	**<0.001**
Biome–Sav Lowveld	-1.882	0.210	**<0.001**
Mixed	-0.149	0.095	0.117
WBLU–Neither	-0.281	0.157	0.074
WBLU–Trophy	0.121	0.119	0.310
WBLU–Both	0.324	0.112	**0.004**

With regards to closely related species that are capable of interbreeding (congeners), seven properties had bontebok *Damaliscus pygargus* and blesbok living in the same extensive areas, 21 had blue and black wildebeest *Connochaetes gnou*, and 10 had plains zebra and Cape mountain zebra *Equus zebra*. In total, 13% (n=30) of properties had mixed one or more of these species' pairs. On state PAs, four had both blue and black wildebeest and three had both plains zebra and Cape mountain zebra.

3.6. Animal numbers and large stock units

The median number of animals per hectare on surveyed properties across all biomes was 0.318 (95% CI: 0.274–0.354) (n=182) or 32 animals per 100 hectare, compared to 0.161 or 16 animals per 100 hectare on state PAs (n=12). Based on a potential range of 17–20.5 million hectares for the total area of wildlife ranches nationally, and the 95% CI values for numbers per hectare, the lower and upper bounds of the total number of herbivores on wildlife ranches in South Africa are 4.66 and 7.25 million individuals.

The mean grazer LSU per hectare on surveyed properties was 0.083 (±0.068) (n=182, median=0.062) (or 8.3 LSU per 100 ha) compared to 0.068 (±0.042) (n=12, median=0.064) on state PAs. Comparisons of our sampled grazer/mixed feeder LSU per ha with predicted agricultural grazing LSU, showed that, overall, 76% of surveyed properties were stocked below their estimated grazing capacity (Figure 5). When separated by mixed farm status, 64% of wildlife only and 86% of mixed farms were stocked below their estimated grazing capacity.

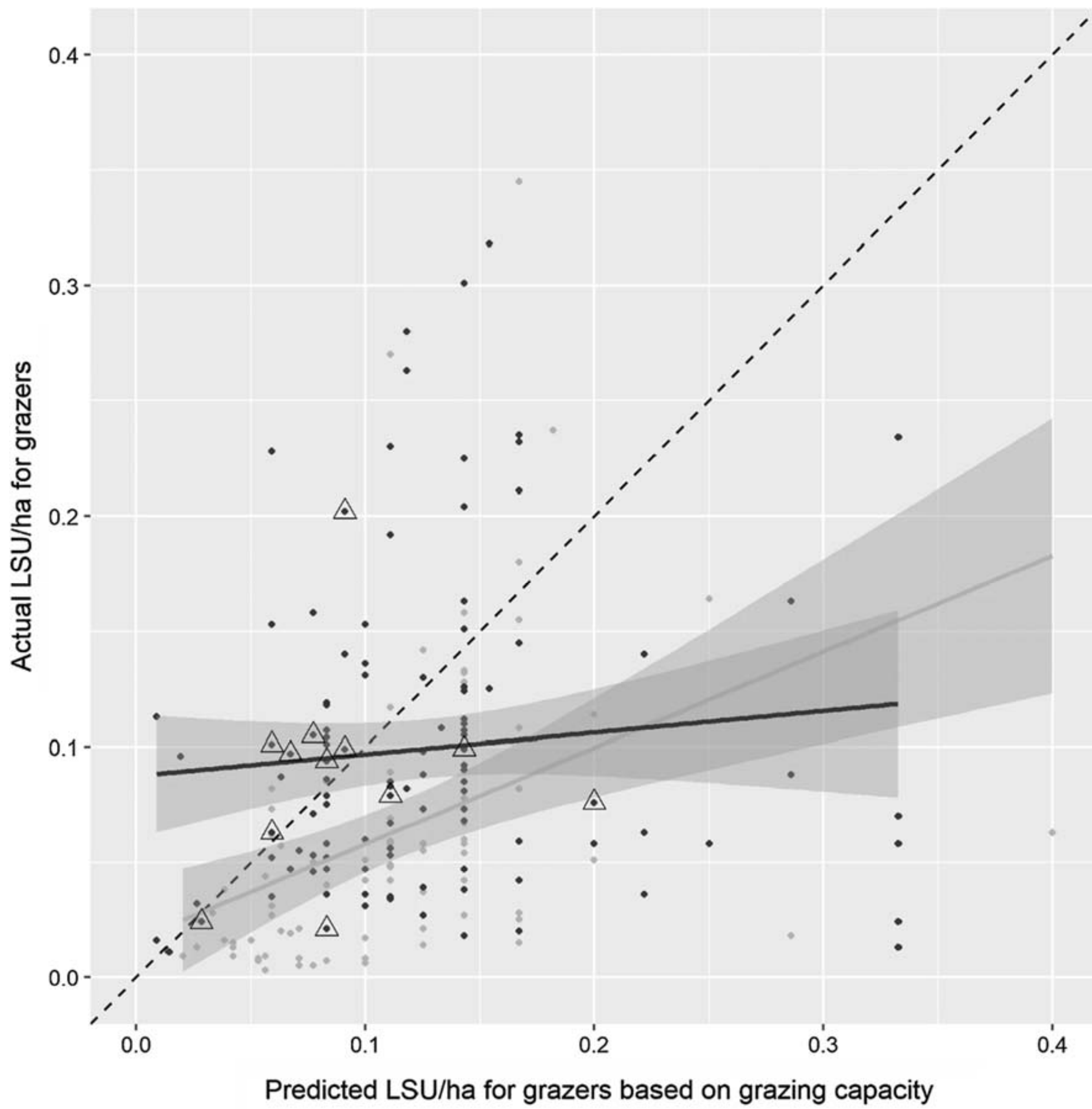

Fig. 5 Large Stock Units/ha of grazers on surveyed properties and PAs against predicted LSU based on grazing capacity. Black dots = wildlife only, grey dots = mixed farms, triangles = state PAs. Black line = linear regression line for wildlife only properties, grey line = linear regression line for mixed farms. Shaded areas represent 95% CI. Diagonal dashed-line represents expected values if the LSU of properties equals the predicted agricultural LSU

3.7. Dietary supplement provision

Seventy-seven percent of participants provided some form of dietary supplement to their ungulates, with 48% providing supplemental food such as lucerne, 52% providing mineral licks, and 33% providing both. While licks were provided all year, there was variation in the extent to which extra food was provided, and most participants only gave food during the dry season or during droughts. Thirty-three percent provided no supplements.

4. Discussion

4.1. Substantial wild ungulate populations on private land

There are no reliable historical estimates of herbivore numbers available for private land in South Africa (Conroy and Gaigher 1982), although one unpublished report suggests that there were approximately 575,000 herbivores across national parks and private land in 1966 (du Toit 2007). Assuming that this is roughly correct, the number of wild herbivores on private land would have been a fraction of this. Our estimate of between 4.66 and 7.25 million herbivores living on wildlife ranches across South Africa, therefore, represents a more than ten-fold increase over 50 years and demonstrates that commercial WBLUs can result in substantial increases in wildlife numbers. We note that our national estimates are subject to uncertainties around the number, size, and location of all wildlife ranches, and around herbivore counting methods.

Trends of increasing wildlife numbers have also occurred on private land in other southern African countries where landholders have been assigned user rights over wildlife. In Namibia, surveys of commercial mixed livestock/wildlife ranchers, showed a 70% increase in wildlife numbers between 1972 and 1992 (Barnes and De Jager 1995), and this trend has been mirrored in community conservancies throughout Namibia since their inception in 1996 (NACSO 2016). Like South Africa, Namibia allows landholders to use wildlife for commercial gain, including consumptive uses like trophy hunting and this is widely credited with creating incentives to conserve wildlife (Taylor et al. 2020). In Zambia, wild ungulate populations increased more than four times on wildlife ranches during the period from 1997–2012, when the area of wildlife ranching concurrently increased about four-fold (Lindsey et al. 2013a). During this same period, wild ungulate populations declined in state PAs across Zambia (Lindsey et al. 2013a). While all land in Zambia is owned by the state, legislation allows for leaseholders to benefit commercially from wildlife.

These wildlife successes stand in stark contrast to the plight of wildlife in many other African countries. Between 1970 and 2005, population abundance time series analysis showed 50% declines in herbivore numbers in eastern Africa and 85% declines in western Africa (Craigie et al. 2010). More recently, Lindsey et al. (2017) found that <50% of savannah PAs had ungulate populations above 50% of carrying capacity. Since 1977, Kenya has experienced a precipitous decline in wildlife populations, both on private land and state PAs, with this decrease possibly being as high as 68% (Norton-Griffiths 2000, 2007; Ogutu et al. 2016). Norton-Griffiths (2000) and Ogutu *et al.* (2016) ascribed this "fundamental institutional failure" to a number of factors including policy failures such as the over-reliance on command and control conservation, institutional failures such as lack of property and user rights, and market failures due to a lack of incentives to keep wildlife. Further contributors to the declines included exponential human population growth, increasing livestock numbers, habitat loss and poaching for bushmeat. Against this general downward trend, however, we recognise some localised recent successes, such as in PAs managed through collaborative management partnerships between NGOs and wildlife authorities, and some community conservation areas (Northern Rangelands Trust).

4.2. The conservation contribution of wildlife ranches to threatened herbivore species

The positive contribution of wildlife ranching to the conservation of threatened herbivore species is substantiated by the fact that all nine of South Africa's indigenous herbivore species that are currently listed as threatened (CR, EN or VU) or Near Threatened on the global IUCN Red List of Threatened Species occurred on our sampled properties and that ranches have significantly more threatened species than state PAs when property/reserve size is controlled for.

The importance of private landowners in the conservation success of the white and black rhinos over the last 50 years is well documented (Clements et al. 2020; IUCN 2020a, b; Knight 2020) and has been attributed to two main factors that incentivised landowners to conserve these species: 1) the opportunity to buy rhinos from state PAs; and 2) policies that allowed high revenues to be generated from limited trophy hunting (Clements et al. 2020). The current poaching crisis that is causing South Africa's rhino populations to decline has disproportionately affected rhinos in state PAs over the last decade, and now private owners own and protect nearly 50% of the county's white rhinos (Clements et al. 2020).

The contribution of wildlife ranches to the successful conservation of other large herbivores is less well known, but worth acknowledging. Across most of Africa, giraffes have undergone a population decline of ~30% over the last three decades (Dunn et al. 2021) and are listed as Vulnerable on the Red List (IUCN 2016). In southern Africa, however, giraffe populations are increasing, even in countries where hunting and trade is legal (Dunn et al. 2021). On the South African Regional Red List assessment giraffes are listed as Least Concern (Deacon and Parker 2016) and our findings of high giraffe occurrence on wildlife ranches emphasises the importance of private land in this conservation success.

The Cape mountain zebra was saved from extinction by farmers in the Cradock area during the 1930s and, more recently, population increases on wildlife ranches have resulted in the status of this species being changed from Vulnerable to Least Concern (Hrabar et al. 2016). While mountain reedbuck (*Redunca fulvorufula*) have undergone a major population decline on state PAs over the last 15 years for unknown reasons (Taylor et al. 2016), the status of this species on private land is uncertain. However, the high prevalence of mountain reedbuck on wildlife ranches may prove to be an important backup for this species if national population declines continue. Similar to Cape mountain zebra, the bontebok was saved from extinction by farmers in the Bredasdorp area and there are now numerous populations on private land (Radloff et al. 2016). However, many of these populations are extralimital and, in this study, all 14 occurrences occurred on properties outside of their natural range. Additionally, there are uncertainties in the genetic purity and wildness of the species on private land (Radloff et al. 2016), which will require monitoring and innovative public-private partnerships.

4.3. Conservation implications of high ungulate numbers on private land

On their own, the growth in ungulate numbers and protection of threatened species are not sufficient indicators of biodiversity conservation success without consideration of other ecological, evolutionary and management factors. Most wildlife ranches cannot be managed like state-funded PAs because they need to be independently financially viable, with profit often being the priority and conservation benefits a secondary spinoff (Taylor et al. 2020). This leads to trade-offs between viability and conservation, with the focus on profit sometimes leading to management actions that diminish the conservation benefits for wildlife.

One immediate question that arises is how wild are these ungulates? While we did not consider this question here, Child et al. (2019) developed a framework to measure the wildness of managed large vertebrate populations and tested this using the same dataset presented in this study. When tested against six species, wildness scores were found to differ significantly among species. Most properties contained both wild and nonwild populations for different species, meaning the same property contained some species that were considered wild and some that were not. Smaller areas generally had lower wildness scores, but the effect was species dependent. These nuances in the conservation contribution of wildlife ranching to species conservation must be mainstreamed into monitoring and reporting. For example, a wildness assessment could be integrated into biodiversity surveys or the provincial permitting process to determine a more qualified estimate of the rewilding value of the wildlife sector at a national scale. Importantly, this would not be to 'punish' the sector but rather to more accurately understand the trade-offs involved between economic development and biodiversity conservation such that more enabling policies and incentives could be designed.

Most private landowners do not have the financial resources to own very large areas of land, while their ability and/or willingness to allow free movement of ungulates onto neighbouring properties is limited. In order for landowners to obtain ownership rights over their wildlife under the Game Theft Act in South Africa (No. 105 of 1991), they have to demonstrate that they have adequate game-proof fencing to prevent escape of species listed on their provincial permits (Blackmore 2020). By design, such fencing restricts the movement of ungulate species (Boone and Hobbs 2004) and, while this aids financial security, it is restrictive in ecological and evolutionary terms because it reduces ecological connectivity (Woodroffe et al. 2014) and gene flow (Hayward and Kerley 2009).

Given that 85% of our surveyed properties had game fences, it is likely that movements of ungulates across property boundaries are restricted. Yet few fences are truly impermeable (Boone and Hobbs 2004; du Toit 2010) and some movement of game through fences is inevitable, with ungulates going over, under or through fences (Boone and Hobbs 2004; du Toit 2010). Movement through fences is quite common, especially where fences are damaged (Pirie et al. 2017). The more permeable a fence is, the less impact it will have on the ecology and evolutionary adaptability of mammals, and we propose that regulations around fencing requirements and how these affect the Game Theft Act be revisited. To incentivise landowners to make their fences more permeable, laws around game ownership will need to accommodate rancher financial needs, including the fact that enclosing wildlife makes it easier to manage. This supports the recommendation by Blackmore (2020), who suggested that the Game Theft Act requires amendments to accommodate potential future needs of wildlife to migrate as a consequence of climate change. In addition to natural movement of animals through fences, wildlife translocations between ranches are an additional mechanism of ungulate movement. This common management tool (La Grange et al. 2010) may mitigate the problem of reduced gene flow (de Jager et al. 2020) but, if not well regulated, increases the risks of introducing extralimital species and diseases (Goss and Cumming 2013), and the accompanying issues of resource competition, hybridisation, and homogenisation, discussed below. Further research is required on the impacts of private translocations.

While restricting movements of ungulates across property boundaries could lead to degradation of rangeland condition, we found that most ranchers did not overstock grazers. The limitations of this finding are that we based the estimated grazing capacity on one location per property, which assumes homogeneous grazing rather than heterogeneous grazing, and that the grazing capacity estimates were calculated for veld in good condition

(Department of Agriculture, Forestry and Fisheries 2016). In reality, herbivores encounter a constantly shifting mosaic of plant production (Peel et al. 1999), and any rangeland system can experience periodic droughts that can result in acute deficits in nutrient intake relative to maintenance requirements (Fynn et al. 2019). As this can lead to population collapses, landowners need to be cognisant of changing climatic conditions. Given that nearly half the ranchers provide supplemental food during droughts or during winter when availability of grazing is low, field vegetation surveys should be used rather than broad scale grazing maps to determine whether a property is overstocked at any particular time.

Another factor that could reduce the conservation benefits of ranching is the presence of extralimital species. During the growth of the wildlife ranching sector, areas previously depleted of wildlife were restocked through reintroductions of species from other areas of the country, and this coincided with introductions of extralimital species because landowners were wanting to increase the attractiveness of their properties to tourists (Castley et al. 2001; Maciejewski and Kerley 2014). Our finding that 85% of participating properties had at least one extralimital species corroborates similar findings from two decades earlier (Castley et al. 2001).

Testing the potential impacts of extralimital species was beyond the scope of our study, but we make the following observations. With regards to the likelihood of resource competition, there is limited evidence for this among African ungulates. One example is a study of nyala (*Tragelaphus angasii*) and bushbuck (*Tragelaphus scriptus*) in three PAs in KwaZulu-Natal where both species coexist. Bushbuck have gone locally extinct in one PA, while in the other two PAs, where nyala numbers are kept down by management culling and leopard *Panthera pardus* predation, bushbuck have persisted (Ehlers Smith et al. 2020). This suggests that bushbuck may tolerate a threshold of nyala densities, above which bushbuck numbers decline. Nyala were the second most common extralimital species in our sample, and the two species coexisted on nearly half the surveyed properties, indicating that landowners should be aware of this potential dynamic and monitor and manage nyala numbers where they are sympatric with bushbuck. It is noteworthy, however, that nyala and bushbuck are naturally sympatric in northern South Africa and in parts of Zimbabwe.

In terms of hybridisation, which can reduce species survival through reduced fertility and gene swamping (Grobler et al. 2018), the translocation of extralimital species has resulted in the placement together of congeners that are not usually sympatric, thus artificially breaking-down historic barriers to reproduction that once kept such species distinct. In South Africa, hybridisation has been documented between blue wildebeest and black wildebeest (Grobler et al. 2018), blesbok and bontebok (van Wyk et al. 2013), and plains zebra and

Cape mountain zebra (Dalton et al. 2017). While it should be acknowledged that the private sector has played an instrumental role in the recovery of black wildebeest (Grobler et al. 2011), bontebok (Radloff et al. 2016) and Cape mountain zebra (Hrabar et al. 2016), all of which were threatened with extinction due to human activities, some translocations have brought them into contact with their congeners and may now be putting them at risk of hybridisation (Grobler et al. 2011). For example, a study of 3000 bontebok and blesbok across South Africa, including both state and private land, revealed that two-thirds of bontebok populations had hybrid bontebok-blesbok individuals within their ranks (van Wyk et al. 2016). Our finding that 13% of surveyed properties had mixed one or more of these species pairings indicates that responsible landowners should take precautions to avoid negative outcomes.

Homogenisation is the gradual replacement of native biotas by locally expanding non-native species that diminishes faunal distinctions between regions (Olden et al. 2004). While this has been shown to occur in plants and fish (McKinney 2005), many aspects of biotic homogenisation remain poorly investigated and the impacts untested (Spear and Chown 2008). The greatest threat for large herbivores may come from non-native species that perform novel functions at the site of introduction, such as in systems that were previously devoid of indigenous large herbivores. As all areas of South Africa had high diversities of ungulates before human interference, it is unclear how significant this risk is from the wildlife ranching sector. Vegetation changes resulting from the introduction of extralimital ungulates are also not well tested, but there are known cases. For example, Giraffe introduced into the south-western Kalahari, a region they never occurred in historically, have been shown to negatively impact the canopy of trees (February et al. 2017). Other examples are limited, so the widespread impact of this is unknown.

Overall, despite the substantial concerns for impacts of extralimital ungulates on biodiversity, the evidence that these impacts are being realised is far from comprehensive (Spear and Chown 2009b). Given that agricultural practices changed the landscape long before wildlife ranching became widespread and that climate change will alter the future geographic range of species, we suggest that, rather than dictate acceptable species distributions based on historic maps, we adopt a policy direction that takes a broader evidence-based approach to defining future distributions. One option might be to develop niche models for each species under climate change forecasts to assess which areas outside of the historical distribution are most suitable for reintroduction and which areas would benefit, from a habitat restoration perspective, from having various functional guilds present. Any such policy changes would still need to account for the potential impacts of resource competition, hybridisation, homogenisation, and changes to vegetation dynamics.

4.4. The impact of trophy hunting

We anticipated that trophy hunting properties might have a wider range of herbivore species and a larger number of extralimital species than ecotourism properties as a strategy to attract foreign hunters, but this was not supported by the results. Instead, species richness and number of extralimital species were similar across trophy hunting and ecotourism properties. We did not examine the potential impacts of trophy hunting on community structure and function of ungulates on wildlife ranches, or the potential evolutionary impacts of selectively harvesting trophy animals, as hypothesised to be potential problems with trophy hunting by Ripple et al (2016). However, given that trophy hunting is widespread on wildlife ranches (Taylor et al. 2020), viewing the ungulate population occurrence and density at a national level suggests that trophy hunting is compatible with conserving ungulate species diversity. The combination of trophy hunting and ecotourism is also commonly found in Namibia, where wild ungulates have also increased (Barnes and De Jager 1995; NACSO 2016).

5. Conclusions

The growth of the wildlife ranching sector has led directly to the conservation of huge numbers of wild herbivores on private land in South Africa, a pattern that is unparalleled on any land tenure system outside southern Africa. This boom is coupled with the protection of all herbivores currently listed as threatened in South Africa. However, the confinement of these animals within fenced properties raises some conservation concerns, which remain to be fully tested. To reduce the negative impacts of fencing, landowners could drop fences between wildlife properties or make fences more permeable to herbivore movements, but these would only be considered if legislative changes or incentives made them feasible. Inducements might include amendments to the Game Theft Act that allow landowners to retain ownership of wildlife with permeable fences, government subsidies that encourage more conservation-oriented management, or the development of a market-based certification scheme that supports good conservation practice through financial benefits. Financial incentives might also encourage the removal of extralimital species where these are detrimental to conservation.

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7. Declaration statements

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All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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