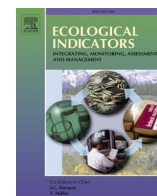


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# Ecological Indicators

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## Leopards and mesopredators as indicators of mammalian species richness across diverse landscapes of South Africa

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### ARTICLE INFO

#### Keywords:

Biodiversity  
Camera-traps  
Conservation  
Indicator species  
Predators  
Mesopredator  
Leopard (*Panthera pardus*)  
Species richness  
Surrogate species

### ABSTRACT

The rapid extinction of species over the past few decades has created a biodiversity crisis. Factors contributing to recent extirpations are linked to increased human population growth, habitat loss and fragmentation, and over-exploitation of wildlife. Only decisive, effective action to combat biodiversity loss can reverse these trends. The use of indicator species as surrogates for biodiversity provides a way to identify areas with high biodiversity so that conservation efforts can be accelerated and supported in those areas. Predators are considered important indicators of healthy, biodiverse ecosystems due to their high trophic level and their direct and indirect interaction with other species. Using camera trap data from 221 cameras set across five vegetation types and five land use zones in South Africa, we evaluated carnivores as potential surrogates for biodiversity. We used the leopard (*Panthera pardus*), and three meso-predators: caracal (*Caracal caracal*), honey badger (*Mellivora capensis*), and black-backed jackal (*Canis mesomelas*), as candidate indicator species. We used mammals captured at the camera traps as a measure of biodiversity referred to as mammalian species richness. The mammalian species richness was highest in the Orange River Nama Karoo vegetation type and in privately owned game reserves. We found that predator sightings were associated with significantly higher mammalian species richness which increased with increasing number of predator species. These findings suggest that the surrogate species concept can be applied to leopard and meso-predators.

### 1. Introduction

Over the past few decades, there has been a precipitous decline in global biodiversity (Johnson et al., 2017; Lanz et al., 2018). Biodiversity loss is mainly due to human-induced changes to the environment, including habitat loss and fragmentation, invasion of non-indigenous species, over-exploitation, and human-caused mortality (Ceballos and Ehrlich, 2002; Gascon et al., 2000; Gibbons et al., 2000). Dirzo et al. (2014) highlighted that the planet loses approximately 11 000 to 58 000 species annually, and currently 33% of the existing vertebrate species are categorised as Endangered (IUCN, 2019). Localised declines of

species and biodiversity have resulted in collapse of ecosystem functions (Brooks et al., 2002; Estes et al., 2011; Woinarskia et al., 2015). Biodiversity is crucial in the functioning of ecosystems and the wellbeing of humanity; loss of biodiversity negatively affects various biogeochemical cycles which ensure sustainability of natural resources (Chapin et al., 2000). With accelerating threats to global biodiversity and resultant collapse of ecosystem functions predicted to occur by 2100 (Sala et al., 2000), there is an urgent need for decisive action to combat declines in biodiversity. Conservationists have proposed to use some species as surrogates for evaluating the status of other species or biodiversity (Burgas et al., 2014; Sergio et al., 2008).

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<https://doi.org/10.1016/j.ecolind.2020.107201>

Received 28 January 2020; Received in revised form 8 November 2020; Accepted 17 November 2020

Available online 5 December 2020

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A surrogate species stands in the place of one or more other species, because it has desirable attributes such as easier measurability, particular sensitivity to threats, or we have a better scientific understanding of its biology. Indicator species are one type of surrogate as are umbrella species or flagship species. Conservationists have long sought surrogates that allow one to focus resources and time on the conservation of the surrogate, which would incidentally then protect many other species. This hypothesis of surrogacy has a mixed record of success (Lawler and White, 2008; Burgas et al., 2014) and overlaps the theory of indicator species (Nally and Fleishman, 2002). Some indicator species are highly sensitive to a threat but are not themselves of concern to conservationists (e.g., water striders) (Jardine et al., 2005). Such indicators often reveal environmental pollutants or eco-physiological health of a habitat or ecosystem, rather than the conservation status of other species. However, there might be overlap in the concepts if an indicator species is measurable, sensitive, well-understood, and of conservation or ecosystem health concern. Then interventions to protect the surrogate indicator might help other species, itself, and provide a measure of success of conserving biodiversity.

Due to intrinsic traits such as large spatial requirements, vulnerability to altered landscapes, and strong predator-prey interactions, carnivores are considered valuable focal species for conservation efforts (Carroll et al., 2001; Carbone and Gittleman, 2002). The role of predators as ecosystem engineers varies depending on many factors (e.g. predator diversity, size, hunting strategy), however there is emerging consensus that predators are crucial to ecosystem health (Schmitz, 2008; Terborgh and Estes, 2010; Estes et al., 2011). Predators exert pressures on their prey and predation risk results in antipredator behaviour among prey species, leading to decreased efficiency in reproduction and foraging (Nakaoka, 2000). When carnivores are removed from a system for long periods their absence has cascading effects on biodiversity on several trophic levels (Terborgh and Estes, 2010). For example, by affecting herbivore movements through predation impacts, carnivores can promote plant growth, which provides habitat for other species and conserves sensitive habitats such as riparian zones (Beyer et al., 2007; Ripple et al., 2014). In some cases, prey species may decline as a result of predation, leaving other species an opportunity to thrive (Estes et al., 2011; Ripple et al., 2014; Silliman and Bertness, 2002). Consequently,

the loss of top predators from ecosystems has led to ecological cascades (Estes et al., 2011; Ripple et al., 2014; Terborgh, 2005) while areas where apex predators remain are associated with high biodiversity (Sergio et al., 2008).

In South Africa, almost all apex predators, such as lion (*Panthera leo*) and spotted hyena (*Crocutta crocutta*) are confined to parcels of fenced areas. Unrestricted by these predator-proof fences, the leopard (*Panthera pardus*) exists across various land use zones where suitable habitat is present, making it the last free-roaming apex predator in South Africa (Ripple et al., 2014). While the leopard is legally protected in South Africa they continue to be persecuted, along with meso-predators. Meso-predators such as caracal (*Caracal caracal*), honey badger (*Mellivora capensis*) and black backed jackal (*Canis mesomelas*) are also free-roaming in South Africa. Carnivores are persecuted due to human-carnivore conflict because of actual or perceived depredation to livestock and game (farmed for hunting and meat) (Lindsey et al., 2009; Treves et al., 2016). These conflicts can have negative impacts on biodiversity at local and regional scales within livestock and game production landscapes as by-catch species are often removed in lethal controls (Estes et al., 2011; Ripple et al., 2014; Rochlitz et al., 2010).

Here we explore the utility of predators as surrogate and indicator species, in a hierarchical fashion. We used data from 221 camera traps set across five survey areas that encompassed five vegetation types and five land use zones (Fig. 1), to determine mammalian species richness as a measure of biodiversity. First, we use measures of the presence of a handful of predator species in hopes of finding ecosystem-specific or habitat-specific indicator(s) of healthy, intact, natural systems in South Africa. If the presence of one or more predator species correlates to the presence of other mammalian biodiversity, we would infer it might be a useful indicator of a biodiverse, healthy vegetation type or land-use category. However, the absence of a predator species does not by itself indicate an unhealthy land unit. Instead, one species might be absent or scarce because a critical resource is missing from that land unit. If all indicators are scarce and other biodiversity is likewise scarce, one might more confidently infer the land unit is degraded and might need restoration. If indicator predator species are missing but other biodiversity is abundant, one might infer that a particular threat to predators is active in that land unit (e.g., lethal predator control). Conversely, if indicator

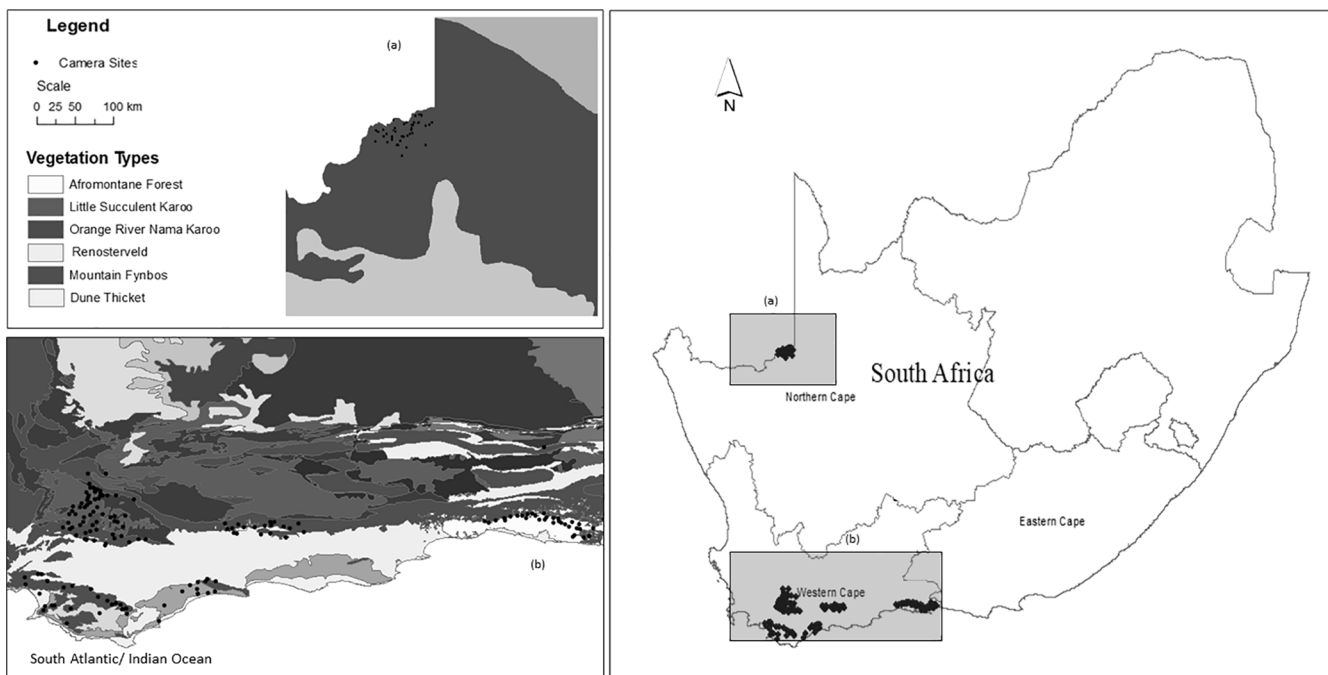


Fig. 1. The distribution of camera trap sites placed across five broad surveyed areas in South Africa. The magnified boxes a) and b) indicate the location of camera traps across the various vegetation types present in the surveyed regions.

predators are abundant but other biodiversity is scarce, one might infer that threats to the other biodiversity (such as over-hunting of prey or transformed landscapes) is present in that unit. The preceding logic might thereby provide a rationale for predators as surrogates. The utility of surrogates in general and the specific use of predators as surrogates may vary in effectiveness as a result of their vulnerability to specific threats versus general threats that affect many other species, and might thus vary among vegetation types and land use zones.

First, we evaluate the correlation between mammalian species richness and the presence of three predator presence categories individually, namely a) leopards (an apex predator), b) 3 mesopredators, and c) all predators combined (predator richness). We test if mammalian species richness varies by vegetation type, and land use. We expect that mammalian species richness will increase significantly with each predator presence categories (leopard, mesopredators and predator richness), and that the surrogacy of the leopard and mesopredators will vary across vegetation types and land uses. We used the strength of correlations to propose predator indicator species in vegetation and land-use types, then discuss possible surrogate roles for conservation intervention.

## 2. Materials and methods

### 2.1. Study area

We surveyed five areas that incorporated five vegetation types and five land use zones, within three provinces of South Africa, namely the Eastern, Western and Northern Cape (Fig. 1). The surveyed areas show variable topography, from coastal zones to mountain peaks with an elevation of >1600 m along the Cape fold mountain range, a long, narrow mountain range running through the Eastern and Western Cape provinces. The Northern Cape is characterised mainly by vast, semi-arid plains. The average annual rainfall varies from 200 mm in Northern Cape to 900 mm in the Mediterranean climate of Western Cape's coastline and forested southern mountain slopes (Mucina and Rutherford, 2006).

### 2.2. Vegetation types

The study area incorporated five broad vegetation types: Afromontane Forest, Fynbos, Orange River Nama Karoo (ORNK), Renosterveld and Succulent Karoo (Fig. 1). Afromontane forests makes up the smallest area of the vegetation types represented in this study, present in only a few southernmost coastal areas, and more patchily in mountain gorges and south-facing slopes (Manning, 2009; Mucina and Rutherford, 2006). Afromontane forests are characterized by a tall, continuous tree canopy which shelters an understory of smaller shrubs and trees. The high rainfall in Afromontane forest results in trees with low nutritional value, therefore these forests host fewer herbivorous species compared to areas with higher nutritional value plants. Fynbos vegetation types form part of the biodiverse Cape Floristic Region. Typical of the southern portion of the region, Fynbos is characteristically dense, fire-adapted shrubland that is seldom more than 3 m high, with a three-layered structure (Mucina and Rutherford, 2006). The canopy is primarily comprised of medium to tall shrubs of the families Proteaceae and Ericaceae, while restios (family Restionaceae) and small shrubs make up the middle layer, and herbaceous bulbs and perennials the understory (Manning, 2009; Mucina and Rutherford, 2006). ORNK falls in a semi-desert region, characterised by low, sparse ground cover comprised of grasses intermixed with karroid shrubs. Succulent Karoo occupies low-lying regions in the rain shadow north of the Cape fold mountains and is characterized by low groundcover, dominated by a variety of dwarf succulents such as of the families Crassulaceae, Euphorbiaceae and Mesembryanthemaceae and is a flora biodiversity hotspot (Manning, 2009; Mucina and Rutherford, 2006). Renosterveld is also part of the Cape Floristic Region and has been highly modified in places, leaving

remnant patches of natural areas. Renosterveld is characterised by *Dicerorhammus rhinocerotis* (renosterbos) and other evergreen, short to medium height dense shrubs, with the understory of herbs and bulbous plants (Mucina and Rutherford, 2006). Fire is rare in the Afromontane forest and both Karoo vegetation types, in contrast to Fynbos and Renosterveld which are fire driven systems (Lubke and van Wijk, 1998).

### 2.3. Land use zones

We surveyed five land use zones namely: forestry plantations, formally protected areas, livestock farms, private game farms and unused land. Forestry plantations exist in the southern regions of the study area, adjacent to Afromontane forest vegetation types where rainfall is typically higher. Forestry plantations are characterised by homogeneous pine plantations (*Pinus sp*) of various ages with the seven-weeks fern (*Rumohra adiantiformis*) dominating the understory. Livestock farms incorporated sheep, cattle and or goats and were fenced with 1.2 m fences. Livestock farms undertook extensive farming practices and occurred across diverse terrain. The farmers were open minded to carnivore conservation and generally employed non-lethal predator control techniques. Private game farms within our survey host various ungulates that may not occur outside of these areas. These areas were typically fenced with high game fences (approximately 2.6 m) to restrict the movement of the game. Formally protected areas are mandated to maintain and improve biodiversity and are thus considered a benchmark for biodiversity and typically exclude livestock production and resource extraction. In the Eastern and Western Cape, the Cape Fold Mountains host parcels of 'unused' land that remained untransformed as a result of the difficult rugged terrain, coupled with vegetation with low nutritional value for livestock and shallow soils that make cultivation unsustainable.

### 2.4. Camera traps

We used data from 221 camera stations set across five sampled areas in the Eastern, Western and Northern Cape provinces of South Africa between 2012 and 2014 (Fig. 1; Table 1). These camera stations were placed across five different vegetation and five land use types described above. We used the number of mammalian species recorded at each camera location as a measure of biodiversity (Gregory et al., 2008; Burgas et al., 2014). We excluded all domestic, and avian species from the analyses to ensure the measure of biodiversity was not inflated. If the same species was photographed at the same site within a 60-minute interval it was considered non-independent and was excluded from the analyses. We removed any cameras that were active for <31 days to allow enough time for more cryptic and low density species to be captured.

**Table 1**

Sampling effort of vegetation types and land use zones across the surveyed areas across South Africa. The duration cameras were active (stdev = standard deviation of the duration), and the total number of pictures used in the analyses. Bold indicates sampling totals for vegetation and land use zones.

	Cam Sites	Duration (Stdev)	Pictures
<b>Vegetation Type</b>	<b>221</b>	<b>157 (62)</b>	<b>22,810</b>
Afromontane Forest	47	303 (87)	6042
Fynbos	86	133 (62)	8041
Little Succulent Karoo	18	132 (58)	1543
Orange River Nama Karoo	37	114 (56)	4456
Renosterveld	33	106 (48)	2728
<b>Land Use</b>	<b>221</b>	<b>167 (84)</b>	<b>22,810</b>
Forestry	20	240 (112)	2361
Game	31	123 (59)	3709
Livestock	43	122 (55)	4313
PA	60	216 (117)	6426
Unused	67	135 (77)	6001

## 2.5. Analysis

We used generalised linear mixed models (GLMM) (Zuur et al., 2009) to evaluate the relationship between mammalian species richness and the presence of leopard, mesopredators, and combined predator richness. We tested the binary indication for leopard presence (1) or absence (0); for mesopredator richness and predator richness we used the accumulation of each predator species present (where 0 = no predators present, 1 = one predator species present, where up to 3 predator species could be detected for mesopredators richness and up to 4 predators in the predator richness category).

To test the correlation between mammalian species richness and each predator category, the mammalian richness values excluded the respective predator species that was present. This ensured the mammalian species richness index was independent of the predator species present. Therefore, we tested the relationship between mammalian species richness with leopard presence; mesopredators and with predator richness in separate models.

Global models initially included vegetation type, land use and survey area as explanatory variables, using the duration each camera was active as the random effect. To check for overdispersion and multicollinearity (variance inflation factor < 5), we used the package 'performance' (Lüdecke et al., 2020). Survey area (VIF 124.60) and vegetation type (VIF 106.95) showed high collinearity and therefore 'survey area' was excluded from models. The random effect in the models (camera trap duration) was employed to account for biases in sample effort (Gillies et al., 2006). We applied the Poisson distribution to the models. We selected the final model:  $\text{glmer}(\text{Species Richness excluding Predator category} \sim \text{Predator category} + \text{Vegetation type} + \text{Land Use} + (1 | \text{Camera Duration}))$ . Where 'predator category' was represented by 1) leopard presence, 2) mesopredator richness or 3) total predator richness, respectively. By using vegetation types and land use zones as covariates, we implicitly tested the hypothesis that relationships between mammalian species richness and predator species detections varied according to the coarse-scale habitat differences in the five sampled sites. We used the package 'lme4' (Bates and Maechler, 2012) in R and R Studio version 1.0.153 (R Core Team, 2020) to fit the GLMMs. To further correct possible biases in sampling design and effort we used species accumulation curves in relation to increasing sampling effort for each vegetation, and land use type using the package 'vegan' (Oksanen et al., 2019) in R Studio (R Core Team, 2020).

## 3. Results

We analysed 22,810 photographs from 221 camera traps across five vegetation types and five land use zones of South Africa (Table 1). Cameras were active for an average of 162 ( $\pm 98$ ) consecutive days per site capturing a total of 43 mammalian species including the smallest antelope in the study area (blue duiker, *Philantomba monticola*) weighing approximately 3.5 kg to the largest terrestrial mammal (elephant, *Loxodonta africana*; Supplementary Table 1). Common predators included caracal, honey badger and leopard which were captured in all five vegetation types. Black-backed jackal were only captured in the ORNK.

### 3.1. Sampling

Sampling was not evenly distributed among vegetation types and land use zones, where the 'succulent karoo' was least sampled and 'fynbos' the most, while in land use 'forestry plantations' was sampled the least and 'unused' the most (Table 1). The species accumulation curves indicated each vegetation type (Supplementary Fig. 1) and land use (Supplementary Fig. 2) had captured species richness adequately.

### 3.2. Predictors of mammalian species richness

We tested the three respective predator categories (leopard,

mesopredators and predator richness), vegetation type, and land use as predictors of mammalian species richness.

Of the 221 camera stations 130 sites detected leopard. Leopard presence had a significant positive relationship to increased species richness ( $\beta = 0.09$ ,  $se = 0.05$ ,  $p = 0.05$ , Table 2; Fig. 2). Mesopredators ( $\beta = 0.19$ ,  $se = 0.03$ ,  $p < 0.001$ , Table 2) and predator richness ( $\beta = 0.16$ ,  $se = 0.02$ ,  $p < 0.001$ , Table 2; Fig. 3) also had a significant positive correlation to increased mammalian species richness. Mammalian species richness was significantly lower where predators were absent (Fig. 3).

Among vegetation types, Afromontane forest hosted the lowest species richness and ORNK the highest (Fig. 4) while among land use zones forestry plantations hosted the lowest species richness and private game reserves the highest (Fig. 5). We examined predator richness against the mean standard error of mammalian species richness in each vegetation type (Fig. 4) and each land use zone (Fig. 5). We found that increased predator richness correlated to increased mammalian species richness across all vegetation types, with succulent karoo showing more variation between the number of predator species and mammalian species richness (Fig. 4). Most land use zones also showed strong correlations between increased predator richness and mammalian species richness with forestry and private game reserves showing the weakest positive correlations (Fig. 5).

## 4. Discussion

Leopard and mesopredator presence had a strong positive correlation with higher mammalian species richness and appear to be reliable surrogates. This was in accordance with other studies using predators such as the wolf (*Canis lupus*) (Ripple and Beschta, 2006), grizzly bear (*Ursus arctos horribilis*) (Berger et al., 2001), and eagle owl (*Bubo bubo*) (Sergio et al., 2004) finding similar results. Secondly, we found that areas with low mammalian species richness were associated with areas where predators are absent, a finding that supports other studies (Ives et al., 2005; Saleem et al., 2012; Sax and Gaines, 2003; Sih et al., 1998). Since none of the predator species were present in the areas with low biodiversity in various habitats, this might infer that these land units are ecologically degraded and may need restoration.

There was a consistent positive association between increased predator richness and significantly higher mammalian species richness across the various vegetation types and land use zones surveyed. This strong correlation could be explained by the different predator species employing resource partitioning (Schoener, 1974). This not only allows the predators to co-exist (Kamler et al., 2012), but results in diverse responses by their prey species leading to a diverse community structure (Kotler and Holt, 1989; Letnic et al., 2012).

However, this correlation is not always the case, and an identified surrogate species in one area may not always be an effective surrogate in another (Ozaki et al., 2005; Sergio et al., 2008). This may be due to changes in community in different areas and could be the result of mechanisms such as threats (e.g. leg-hold traps, poisoning and indiscriminate hunting) being present or critical resources being absent thereby limiting species (Menge and Olson, 1990). In the semi-arid succulent karoo vegetation type, we found oscillations between the mammalian species richness and the escalating number of predator species. This may suggest there are limited resources available, or there may be threats present that impact some predator species and not others. As such, the low detection of black-backed jackal among surveyed areas may be explained by patterns of persecution and local extirpation of the species (Ripple et al., 2014; Kamler et al., 2013).

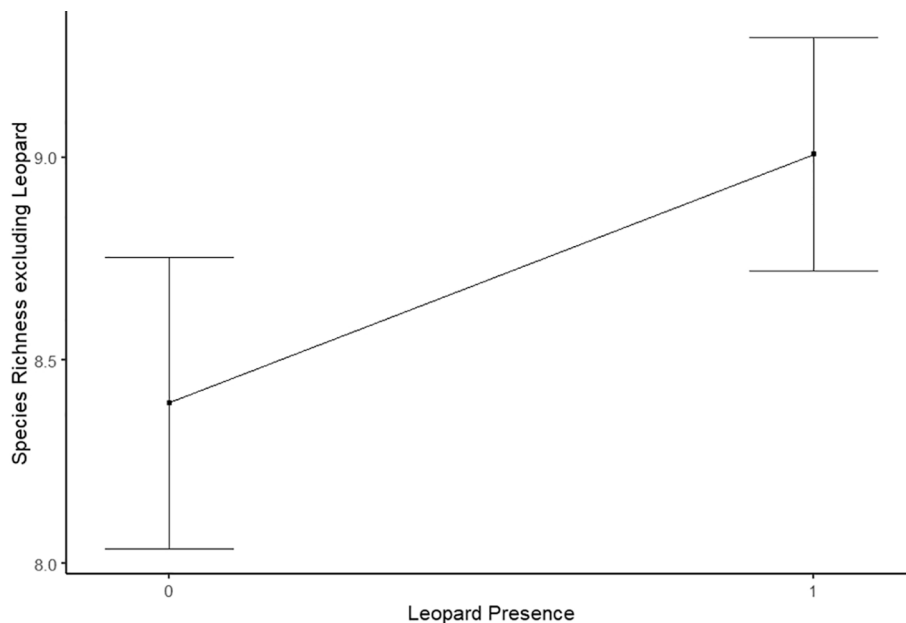
Interestingly, we found that predators also indicated higher mammalian species richness in highly fragmented vegetation types such as renosterveld (Topp and Loos, 2019) and in areas where we observed lower mammalian species richness (i.e. Afromontane forests, and forestry plantations) compared to other sites. This supports the notion that predators may be particularly useful as indicator species in



**Table 2**

Final generalised linear mixed models testing the relationship between mammalian species richness and three predator categories: 1) leopard presence, 2) predator richness and 3) mesopredators richness, land use zones and vegetation types. Significance level of bold  $p \leq 0.05$  and the AICc for model fit for small sample size.

Model	Variables	Est.	S.E.	z val.	p	AICc
<b>Leopard Presence + Land Use + Vegetation Type</b>	Intercept (Forestry)	1.95	0.09	20.70	< <b>0.001</b>	1176.84
	Leopard Presence	0.09	0.05	1.92	<b>0.05</b>	
	Game	0.15	0.12	1.23	0.22	
	Livestock	0.11	0.11	1.01	0.31	
	Protected Area	0.03	0.09	0.30	0.76	
	Unused	-0.01	0.10	-0.12	0.91	
	Fynbos	0.09	0.07	1.35	0.18	
	Succulent Karoo	0.14	0.11	1.31	0.19	
	Orange River Nama Karoo	0.28	0.07	1.69	<b>0.01</b>	
	Renosterveld	0.11	0.11	1.57	0.23	
<b>Predator Richness + Land Use + Vegetation Type</b>	Intercept (Forestry)	1.52	0.11	13.84	< <b>0.001</b>	1075.67
	Predator Richness	0.16	0.03	5.89	< <b>0.001</b>	
	Game	1.65	0.11	16.80	< <b>0.001</b>	
	Livestock	0.16	0.03	5.89	< <b>0.001</b>	
	Protected Area	0.42	0.10	4.04	< <b>0.001</b>	
	Unused	0.24	0.11	2.38	<b>0.02</b>	
	Fynbos	1.49	0.08	17.88	< <b>0.001</b>	
	Succulent Karoo	0.15	0.03	5.87	< <b>0.001</b>	
	Orange River Nama Karoo	0.23	0.07	3.19	< <b>0.001</b>	
	Renosterveld	0.26	0.11	2.62	<b>0.01</b>	
<b>MesoPredators + Land Use + Vegetation Type</b>	Intercept (Forestry)	1.69	0.10	16.84	< <b>0.001</b>	1090.02
	MesoPredators	0.19	0.03	6.10	< <b>0.001</b>	
	Game	0.10	0.12	0.81	0.42	
	Livestock	-0.02	0.11	-0.20	0.84	
	Protected Area	0.01	0.10	0.11	0.91	
	Unused	-0.07	0.10	-0.69	0.49	
	Fynbos	1.69	0.07	23.62	< <b>0.001</b>	
	Succulent Karoo	0.19	0.03	6.06	< <b>0.001</b>	
	Orange River Nama Karoo	0.45	0.11	4.14	< <b>0.001</b>	
	Renosterveld	0.16	0.09	1.79	0.07	



**Fig. 2.** The correlation of leopard absence (0) and presence (1) in relation to mammalian species richness with 95% confidence intervals using data from 221 camera traps set across five survey areas in South Africa.

fragmented landscapes, and in large-scale conservation programmes (Burgas et al., 2014) where the biodiversity of different regions could be assessed through the monitoring of the presence of predators. This is especially useful in altered landscapes where general biodiversity is low, yet the presence of a predator would indicate above average local biodiversity and areas of higher conservation value.

Among land use zones, private game reserves had the highest mammalian species richness followed by livestock farms. The

aforementioned is likely due to the eco-tourism objectives on private game reserves to host diverse ungulate species that may not occur outside these areas. The relatively high mammalian species richness on livestock farms was unexpected, however low intensity livestock farming does support high mammalian biodiversity elsewhere (Signal and McCracken, 1996). Furthermore, this may reflect a selection bias in this land use category, as this survey was welcomed by the owners, who, by facilitating our research may be more tolerant of predators and

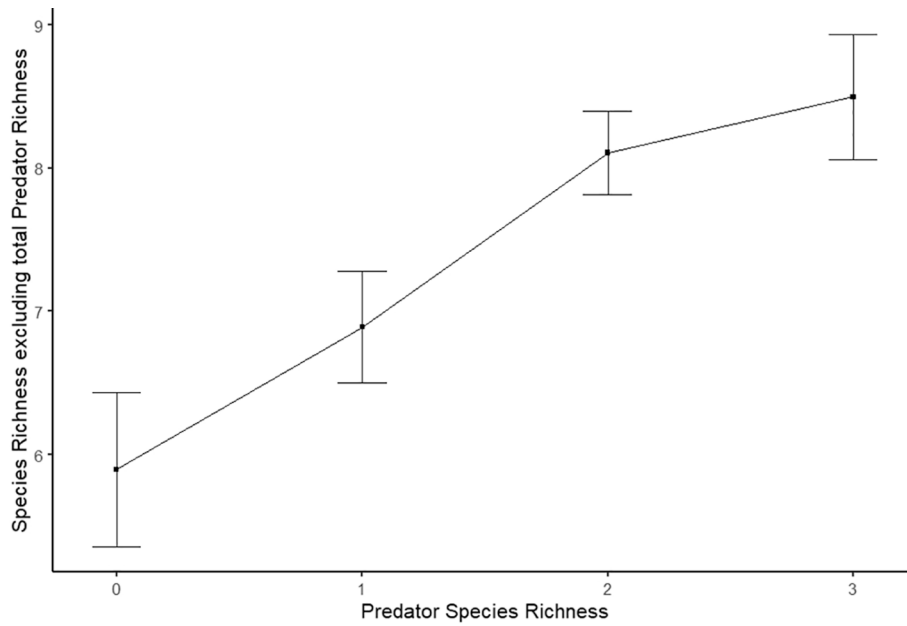


Fig. 3. The correlation of predator species richness (number of predator species present) in relation to increasing number mammalian species with 95% confidence intervals using data from 221 camera traps set across five survey areas in South Africa.

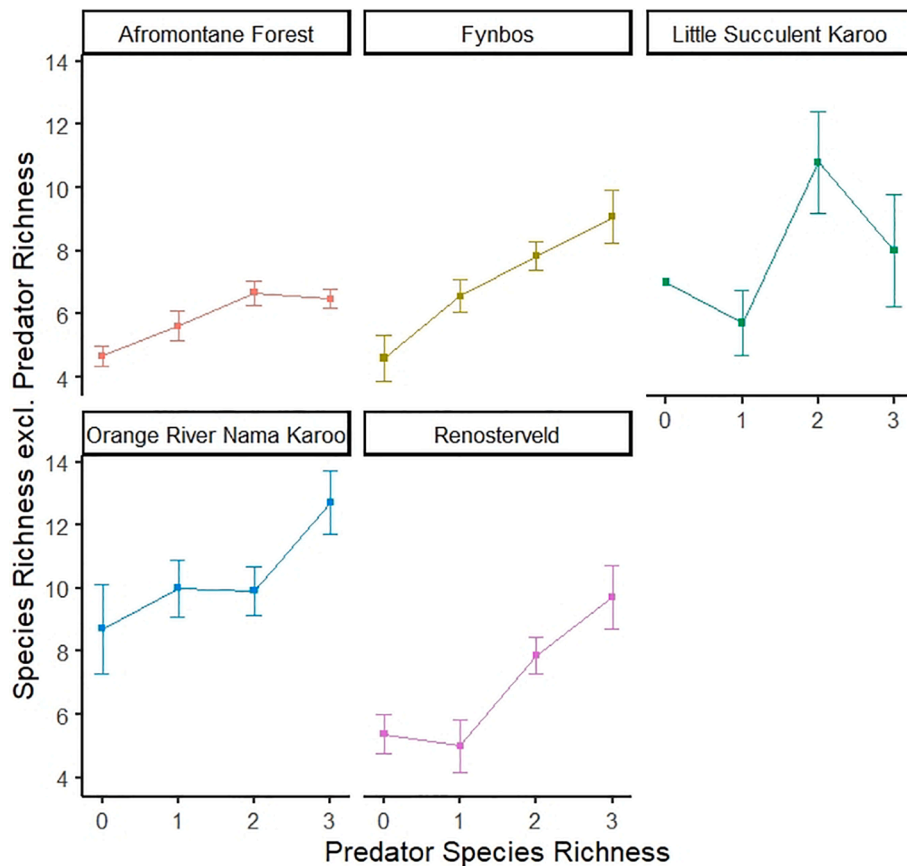


Fig. 4. Summary plots (mean  $\pm$  se) of mammalian species richness in relation to predator species richness (number of predator species present) in each of the surveyed vegetation types: Afromontane forest, Fynbos, Succulent Karoo, Orange River Nama Karoo and Renosterveld.

wildlife. Future research aimed at comparing species richness where predators are tolerated versus human-predator conflict farms could provide insight to this finding. Non-the-less, the high mammalian species richness observed on private land indicates the important role these

landscapes have in promoting and conserving biodiversity.

While surrogate properties for predators in relation to mammalian species richness appear to be valid, predators are often considered pests. Their high metabolic demands result in wide-ranging behaviours,

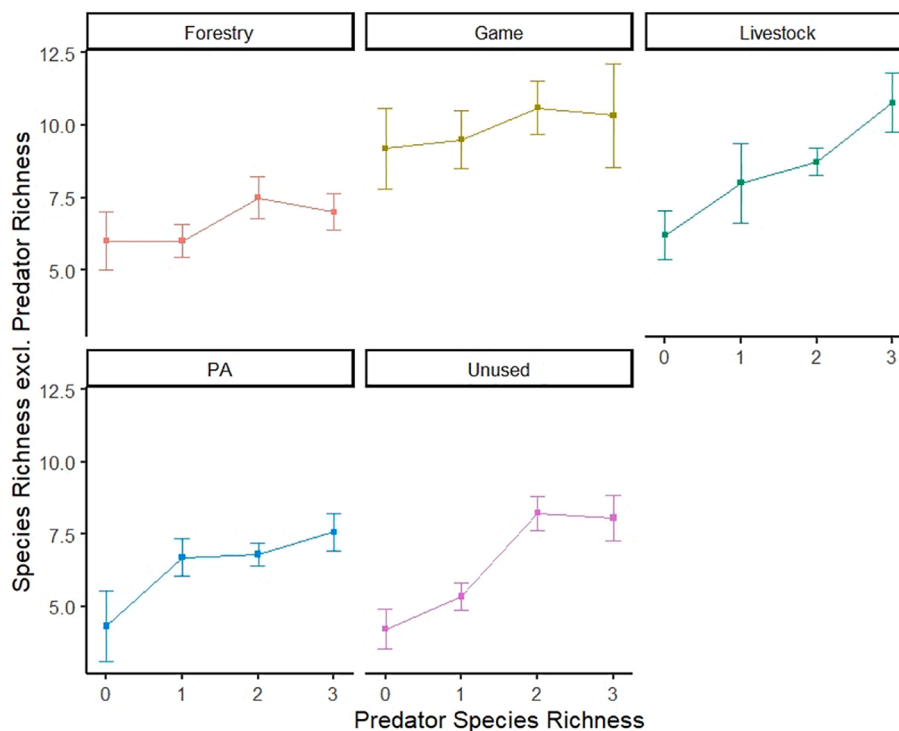


Fig. 5. Summary plots (mean  $\pm$  se) of mammalian species richness in relation to predator species richness (number of predator species present) in each of the surveyed land use zones: Forestry plantations, Game Farms, Livestock, Protected areas (PA) and 'Unused' land use zones.

placing them in various land use zones and into contact and conflict with people. Our findings support that private land is important for carnivore conservation and biodiversity. However, indiscriminate lethal carnivore management tools are commonly employed and implemented over vast areas to remove predators (McManus et al., 2015). These tools are also detrimental to non-target mammalian species (Rochlitz et al., 2010). Since the power of indicator species depends on detectability, where human-wildlife conflict exists, persecuted species may be low or locally extirpated, preventing predators as indicators in highly impacted regions. Mitigating human-carnivore conflict is therefore important to biodiversity conservation efforts (Treves et al., 2016). To increase tolerance toward predators in conflict areas, campaigns aimed at highlighting the strong correlation predators have with higher mammalian species richness could foster tolerance and promote biodiversity-friendly farming practices.

We considered caveats in interpreting the results of our analyses. For example, in a broader context, species richness indices may not adequately represent rare and threatened species. However, while rarity of species could have resulted in poor detection, our survey encompassed diverse environments, thereby increasing the likelihood of capturing species in more narrow niche requirements. Furthermore, it will be beneficial to better understand how lethal and non-lethal predator controls impact mammalian species richness.

## 5. Conclusion

The continual and rapid decline of biodiversity at local and global scales requires informed and effective responses by policy makers, conservationists and society to change the course of survival for species. Areas of high biodiversity need to be conserved (Rodrigues and Brooks, 2007). Predators regulate species; require diversity of prey species; are vulnerable to altered habitats they are considered appropriate surrogates for biodiversity (Dalerum et al., 2008; Sergio et al., 2008). While predators are persecuted, they are useful in public campaigns as flagship species to raise awareness (Carroll et al., 2001). Their ability to occupy various environments and their association with higher

biodiversity across diverse land uses, makes them useful surrogate species in the identification of high mammalian species richness areas (Sergio et al., 2008). Using predators as surrogates could also contribute to changing the narrative of human-carnivore conflict. These results are relevant for conservation practitioners and government conservation agencies, particularly when looking to identify high mammalian species richness areas, or in the establishment or enlargement of protected areas, or in conservation actions fostering connectivity of biodiversity patterns and processes.

## CRedit authorship contribution statement

**Thulani Tshabalala:** Methodology, Writing - review & editing, Writing - original draft, Formal analysis. **Jeannine McManus:** Conceptualization, Writing - review & editing, Supervision, Software, Investigation, Formal analysis, Writing - original draft. **Adrian Treves:** Writing - review & editing, Methodology. **Vusani Masocha:** Software, Validation, Visualization. **Steve Faulconbridge:** Writing - review & editing. **Matthew Schurch:** Writing - review & editing. **Stefan Goets:** Writing - review & editing. **Bool Smuts:** Investigation, Writing - review & editing, Funding acquisition, Project administration.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We would like to extend our gratitude to the funders of this study: National Department of Environment, Forestry and Fisheries, Development Bank of Southern Africa, Global Environmental Facility, Green Fund, United Nations Environmental Program, United Nations Development Program, Henry and Iris Englund Foundation, National Lotteries Distribution Trust Fund, Mones Michaels Trust, Tamarisk Trust, ABAX

Foundation, Timothy Allsop, Brad Banducci, Ishmail Bhorat and Arne Hanson. We sincerely thank the farmers, South African National Parks, Eastern Cape Parks and Tourism Authority, Eastern Cape Department of Economic Development and Environmental Affairs, Northern Cape Department of Environment and Nature Conservation, and Cape Nature for allowing us to conduct research on their properties. We are also grateful to James Harrison who provided insightful comments that improved the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107201>.

## References

- Bates, D., Maechler, M., 2012. lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999999-0.
- Berger, J., Stacey, P.B., Bellis, L., Johnson, M.P., 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. *Ecol. Appl.* 11, 947–960.
- Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S., 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecol. Appl.* 17, 1563–1571.
- Bignal, E.M., McCracken, D.L., 1996. Low-intensity farming systems in the conservation of the countryside. *J. Appl. Ecol.* 413–424.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923.
- Burgas, D., Byholm, P., Parkkima, T., 2014. Raptors as surrogates of biodiversity along a landscape gradient. *J. Appl. Ecol.* 51, 786–794.
- Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. *Science* 295, 2273–2276.
- Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the rocky mountain region. *Ecol. Appl.* 11, 961–980.
- Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. *Science* 296, 904–907.
- Chapin 3rd, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Dalerum, F., Somers, M.J., Kunkel, K.E., Cameron, E.Z., 2008. The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodivers. Conserv.* 17, 2939–2949.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. *Science* 345, 401–406.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* 333, 301–306.
- Gascon, C., Williamson, G.B., da Fonseca, G.A.B., 2000. Receding forest edges and vanishing reserves. *Science* 288, 1356–1358.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50, 653–666.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., Jerde, C.L., 2006. Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* 75, 887–898.
- Gregory, R.D., Voříšek, P., Noble, D.G., Van Strien, A., Klvaňová, A., Eaton, M., Gmelig Meyling, A.W., Joys, A., Foppen, R.P.B., Burfield, I.J., 2008. The generation and use of bird population indicators in Europe. *Bird Conserv. Int.* 18, S223–S244.
- IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-3. <http://www.iucnredlist.org>. Downloaded on 20 December 2020.
- Ives, A.R., Cardinale, B.J., Snyder, W.E., 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.* 8, 102–116.
- Jardine, T.D., Al, T.A., MacQuarrie, K.T., Ritchie, C.D., Arp, P.A., Maprani, A., Cunjak, R.A., 2005. Water striders (family Gerridae): mercury sentinels in small freshwater ecosystems. *Environ. Pollut.* 134, 165–171.
- Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the anthropocene. *Science* 356, 270–275.
- Kamler, J.F., Stenkewitz, U., Klare, U., Jacobsen, N.F., Macdonald, D.W., 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. *J. Wildl. Manag.* 76 (6), 1241–1253.
- Kamler, J.F., Stenkewitz, U., Macdonald, D.W., 2013. Lethal and sublethal effects of black-backed jackals on cape foxes and bateared foxes. *J. Mammal.* 94, 295–306. <https://doi.org/10.1644/12-MAMM-A-122.1>.
- Kotler, B.P., Holt, R.D., 1989. Predation and competition: the interaction of two types of species interactions. *Oikos* 256–260.
- Lanz, B., Dietz, S., Swanson, T., 2018. The expansion of modern agriculture and global biodiversity decline: an integrated assessment. *Ecol. Econ.* 144, 260–277.
- Lawler, J.L., White, D., 2008. Assessing the mechanisms behind successful surrogates for biodiversity in conservation planning. *Anim. Conserv.* 11, 270–280.
- Letnic, M., Ritchie, E.G., Dickman, C.R., 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biol. Rev.* 87 (2), 390–413.
- Lindsey, P.A., Románach, S.S., Davies-Mostert, H.T., 2009. The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. *J. Zool.* 277, 99–105.
- Lubke, R.A., van Wijk, Y., 1998. Terrestrial plants and coastal vegetation. In: Lubke, R.D., de Moor, I. (Eds.), *Field Guide to the Eastern and Southern Cape Coasts Cape Town*. University of Cape Town Press.
- Lüdecke, D., Makowski, D., Waggoner, P. and Patil, I., 2020. Package 'performance'. Manning, J., 2009. *Field Guide to Flowers of South Africa, Lesotho and Swaziland*. Struik Naure, Cape Town.
- McManus, J.S., Dickman, A.J., Gaynor, D., Smuts, B.H., Macdonald, D.W., 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human-wildlife conflict mitigation on livestock farms. *Oryx* 49 (4), 687–695.
- Menge, B.A., Olson, A.M., 1990. Role of scale and environmental factors in regulation of community structure. *Trends Ecol. Evol.* 5, 52–57.
- Mucina, L., Rutherford, M.C. (Eds.), 2006. *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, South Africa.
- Nakaoka, M., 2000. Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. *Ecology* 81, 1031–1045.
- Nally, R., Fleishman, E., 2002. Using 'indicator' species to model species richness: model development and predictions. *Ecol. Appl.* 12, 79–92.
- Oksanen, J., Guillaume Blanchet, F., Friendly, Michael, Kindt, Roeland, Legendre, Pierre, McGinn, Dan, Minchin, Peter R., O'Hara, R.B., Simpson, Gavin L., Solymos, Peter, Henry, M., Stevens, H., Szoecs, Eduard, Wagner, Helene, 2019. *vegan: Community Ecology Package*. R package version 2.5-6.
- Ozaki, K., Isono, M., Kawahara, T., Iida, S., Kudo, T., Fukuyama, K., 2005. A mechanistic approach to evaluation of umbrella species as conservation surrogates. *Conserv. Biol.* 20, 1507–1515.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.
- Ripple, W.J., Beschta, R.L., 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biol. Conserv.* 133, 397–408.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241–1248.
- Rochlitz, I., Pearce, G., Broom, D., 2010. *The Impact of Snares on Animal Welfare*. University of Cambridge Press, Cambridge, UK.
- Rodrigues, A.S.L., Brooks, T.M., 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu. Rev. Ecol. Syst.* 38, 713–737.
- Sala, O.E., Stuart Chapin, F., III, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M.n., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Saleem, M., Fetzer, I., Dormann, C.F., Harms, H., Chatzinotas, A., 2012. Predator richness increases the effect of prey diversity on prey yield. *Nat. Commun.* 3, 1305.
- Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18, 561–566.
- Schmitz, O.J., 2008. Herbivory from individuals to ecosystems. *Annu. Rev. Ecol. Syst.* 39, 133–152.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F., 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Syst.* 39, 1–19.
- Sergio, F., Marchesi, L., Pedrini, P., 2004. Integrating individual habitat choices and regional distribution of a biodiversity indicator and top predator. *J. Biogeogr.* 31, 619–628.
- Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* 13, 350–355.
- Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. *Proc. Natl. Acad. Sci. USA* 99, 10500–10505.
- Terborgh, J., 2005. The green world hypothesis revisited. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, DC, pp. 82–99.
- Terborgh, J., Estes, J.A., 2010. *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*. Island Press, Washington, DC.
- Topp, E., Loos, J., 2019. Fragmented landscape, fragmented knowledge: a synthesis of renosterveld ecology and conservation. *Environ. Conserv.* 46, 171–179.
- Traves, A., Krofel, M., McManus, J., 2016. Predator control should not be a shot in the dark. *Front. Ecol. Environ.* 14, 380–388.
- Woinarskija, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proc. Natl. Acad. Sci.* 112, 4531–4540.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.