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# Spatio-temporal use of multifunctional anthropogenic landscapes by African mammals : testing the principle of anthropodependence

Alice Bernard

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# THESE de DOCTORAT DE L'UNIVERSITE CLAUDE BERNARD LYON 1

**Ecole Doctorale 341  
Évolution, Écosystèmes, Microbiologie, Modélisation**

**Discipline : Ecologie**

Soutenue publiquement le 07/07/2023, par :  
**Alice Bernard**

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## **Utilisation spatio-temporelle des paysages anthropisés multifonctionnels par les mammifères africains. Tester le principe d'anthropodépendance**

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# Résumé substantiel en Français

## Introduction

L'un des objectifs de la 15<sup>ème</sup> conférence des Parties pour la Biodiversité consiste à protéger 30% des terres et des mers de la planète et restaurer 30% des écosystèmes d'ici à 2030. L'Afrique étant confrontée à des compromis importants entre la protection de la biodiversité et la réduction de la pauvreté, des chercheurs s'inquiètent de la manière dont les mesures vont être appliquées (Obura et al., 2021). Ils proposent de « partager » la Terre et les océans, en créant des espaces où la faune et les humains pourraient vivre ensemble (concept de « Shared Earth »), afin de connecter les gens et la nature plutôt que de les séparer, comme cela a historiquement été le cas, notamment sur le continent africain (Blanc, 2020; Obura et al., 2021). Ces espaces partagés assureraient aussi une meilleure connectivité entre les aires protégées afin de développer un réseau efficace permettant le lien entre les diverses populations d'espèces sauvages (Rodrigues & Cazalis 2020; Brennan et al. 2022). Les populations humaines locales pourraient devenir partie prenante des mesures de conservation (Obura et al., 2021). Pour que cette stratégie de conservation soit viable, il faut cependant comprendre si la faune sauvage est en mesure d'utiliser les environnements anthropisés. Plusieurs études ont mis en avant les effets négatifs sur certains mammifères des perturbations d'origine humaine, liés directement ou indirectement (habitats transformés, développement urbain) à leur présence (Sévêque et al., 2020; Suraci et al., 2021). Hulme-Beaman et al. (2016) ont développé un modèle théorique qui classe les espèces en quatre groupes en fonction de leur dépendance aux ressources alimentaires d'origine humaine et leur niche spatiale. Les espèces anthropodépendantes utilisent les environnements humains et ont un régime alimentaire majoritairement d'origine anthropique ; les anthropophiles ont une part de leur régime d'origine anthropique ; les synanthropes utilisent les paysages modifiés par les humains et les anthropophobes évitent tout ce qui touche aux humains. Les espèces modifient souvent leur niche temporelle pour éviter les rencontres directes avec les humains, tout en utilisant le même territoire qu'eux (Gaynor et al., 2018). La capacité des espèces à adapter leur réponse face à ces nouveaux environnements serait fonction de leur écologie et de leurs traits d'histoire de vie, tels que leur poids, leur longévité ou encore la flexibilité de leur régime alimentaire (Santini et al., 2019). C'est dans ce contexte que j'ai conduit mes travaux de thèse, dont l'objectif a ainsi été de documenter l'utilisation spatio-temporelle par les mammifères sauvages des espaces modifiés par les humains et de comprendre les traits leur permettant de s'y maintenir, en testant les hypothèses du modèle théorique proposé par Hulme-Beaman et al. (2016) sur l'anthropodépendance. Je me suis concentrée sur les mammifères, car on s'attend à ce qu'ils répondent différemment à des changements de leur milieu, du fait de leur

diversité de taille, de régime alimentaire et d'écologie. Pour ce faire, j'ai réalisé le terrain de mon doctorat en Afrique du Sud, dans le paysage mosaïque de la municipalité de le Garden Route, entremêlant parc national, végétation naturelle non protégée et habitats transformés (agriculture, plantations, espaces urbains). Ce site a été classé réserve de biosphère par l'UNESCO. Il s'agit donc d'un site privilégié pour tester des solutions visant à concilier conservation et gestion durable de la biodiversité. Mes travaux s'appuient sur deux méthodes de suivis des mammifères : les pièges photographiques et une enquête en ligne pour répondre à mon objectif principal en 3 chapitres qui sont décrits ci-dessous.

**Chapitre 1** : Utilisation d'une méthode classique, les pièges photographiques, pour étudier l'utilisation spatio-temporelle des mammifères afin de documenter l'anthropodépendance

**Quel est la hauteur optimale des pièges photographiques pour détecter les interactions entre les mammifères sauvages et les activités humaines ?**

Dans un premier manuscrit, nous avons testé la hauteur optimale pour photographier les interactions homme et faune sauvage à l'aide de pièges photographiques. Nous avons analysé des données provenant de pièges photographiques installés à deux hauteurs différentes : 130 cm au-dessus du sol (étude sur les humains) et 50 cm (étude sur les mammifères) pour comparer la détection des mammifères et humains. Les pièges photographiques des deux hauteurs différentes ont été positionnés sur le même arbre, le long de sentiers, pendant 5 mois et sur 5 sites du parc national. Nos analyses ont montré que les pièges photographiques positionnés à 50cm au-dessus du sol détectent plus de petites espèces, en particulier la nuit. Ces derniers semblent détecter la plupart des activités humaines, avec une détection légèrement inférieure pour les humains, en comparaison avec les pièges positionnés plus haut. Nous avons donc décidé d'utiliser la hauteur de 50 cm pour notre collecte de données par pièges photographiques.

**Les mammifères africains adaptent-ils leurs activités spatio-temporelles en fonction des humains dans les paysages anthropisés?**

Dans un second manuscrit, nous nous sommes intéressés à la réponse spatio-temporelle des mammifères africains dans les paysages anthropisés et aux perturbations d'origine humaine. En effet, pour survivre dans des paysages dominés par l'homme, les mammifères doivent être capables de s'adapter à divers changements d'origine anthropogénique. Pour ce faire, j'ai déployé 75 pièges photographiques sur un an, en suivant le protocole standardisé « Snapshot Safari South Africa » (Pardo et al., 2021). Les pièges ont été posés dans les zones naturelles/protégées du Parc National de la Garden Route et dans les zones anthropisées

environnantes, en collaboration avec les services scientifiques du parc national, entre février 2021 et mai 2022. Nous avons testé l'utilisation de l'habitat par les mammifères, au cours de deux saisons contrastées (hiver et été), en fonction de diverses utilisations des sols (forêt naturelle et zones cultivées) et perturbations humaines (distance aux infrastructures et densité de routes). Nous avons ensuite mesuré le chevauchement de l'activité temporelle des mammifères avec celle des humains dans des zones à faibles et fortes perturbations d'origine humaine (faible et forte densité de routes, proximité et éloignement des infrastructures humaines), afin d'évaluer la sensibilité à la présence humaine et aux perturbations associées. Nos résultats ont montré la diversité des stratégies développées par les mammifères avec des espèces dépendantes des habitats naturels (e.g. céphalophe bleu, *Philantomba monticola*) et d'autres plus tolérantes aux perturbations humaines (e.g. caracal, *Caracal caracal*), suggérant des coûts-bénéfices différents, comme envisagé par les hypothèses d'anthropodépendance. La majorité des espèces réduisent le chevauchement temporel de leur activité avec celle des humains dans les zones à forte densité de routes, alors que les changements associés à la distance aux infrastructures sont plus faibles. La combinaison d'information sur l'utilisation de l'habitat et les réponses temporelles aux perturbations humaines s'est avérée utile pour mieux comprendre les réponses des espèces aux caractéristiques anthropiques.

**Chapitre 2 :** Utilisation des connaissances écologiques locales afin de décrire le paysage à l'échelle des propriétés privées et la disponibilité des ressources anthropiques pour documenter l'anthropodépendance

**Peut-on évaluer l'anthropodépendance des grands mammifères vis-à-vis des paysages anthropisés à l'aide de connaissances écologiques locales ?**

Dans un troisième manuscrit, nous avons conçu et mis en ligne une enquête destinée aux résidents de la zone d'étude (e.g. agriculteurs, forestiers, habitants), afin d'étudier l'effet des caractéristiques de propriétés (disponibilité et type de ressources anthropiques, intégrité et le type d'habitats naturels, perturbations structurelles et interférences) sur la présence des mammifères sauvages. Cette étude a été validée par le comité d'éthique humaine de l'Université Nelson Mandela (H20-SCI-SRU-002). Cette méthode permet de maximiser la collecte de données avec un protocole reproductible et peu coûteux sur un temps court. Nous avons obtenu 247 réponses qui concordent avec les résultats obtenus grâce aux données issues de pièges photographiques et montrent que l'utilisation de l'espace anthropisé est dépendante des espèces. Certaines espèces comme le babouin (*Papio ursinus*) sont attirées par les ressources anthropiques, alors que la dépendance aux habitats naturels est encore mis en évidence pour le céphalophe bleu. Les résultats suggèrent le rôle positif de la préservation de parcelles de végétation naturelle sur les propriétés privées pour la

conservation, des mammifères. Les connaissances écologiques locales fournissent des informations complémentaires à celles des pièges photographiques en documentant précisément les pratiques locales, les ressources disponibles et les perceptions des résidents sur la faune sauvage.

**Chapitre 3 :** Combiner les méthodes pour comprendre l'écologie et de l'anthropodépendance des mammifères dans les paysages anthropisés

**Peut-on combiner les connaissances écologiques locales et les données des pièges photographiques pour étudier la présence des mammifères africains dans les paysages anthropisés?**

Dans un quatrième manuscrit, nous avons comparé les données de présence et absence obtenues à l'aide de pièges photographiques à celles recueillies par l'enquête en ligne. Les deux méthodes, ont permis de détecter respectivement les 15 espèces de la zone, avec une espèce détectée seulement selon l'enquête, le céphalophe commun (*Sylvicapra grimmia*). Il y avait plus de concordances sur les détections entre les deux méthodes pour les grandes espèces, que pour les petites espèces. En particulier, les mangoustes étaient difficiles à identifier par les participants à l'enquête. La combinaison des méthodes permet cependant de confirmer l'absence de certaines espèces suggérées par les pièges photographiques et de valider les présences indiquées par l'enquête. Les personnes ayant de bonnes connaissances naturalistes semblent ainsi être de bonnes sentinelles pour le suivi des espèces de mammifères. En gardant à l'esprit les contraintes et limites de chaque méthode, les combiner offre une meilleure image de la communauté de mammifères dans les paysages anthropisés. La combinaison des méthodes permet aussi d'augmenter la couverture spatiale et le nombre de données, tout en impliquant diverses parties prenantes dans le processus scientifique pour répondre à des questions de conservation.

**Quels sont les traits d'histoire de vie qui permettent aux mammifères africains d'utiliser les paysages anthropisés?**

Dans le cinquième manuscrit nous avons combiné les deux méthodes précédemment utilisées, afin d'identifier les traits permettant aux espèces de persister dans les milieux anthropisés. Nous nous sommes focalisé sur les traits d'histoire de vie relatifs au régime alimentaire (type et diversité de ressources consommées) et aux stratégies r/K (longévité, durée de gestation, âge de maturité sexuelle, taille de la portée et masse corporelle). Nos résultats ont confirmé que la présence de mammifères dans les habitats modifiés par l'homme était favorisée par des traits spécifiques. Les zones fortement modifiées par les humains étaient plus favorables aux espèces généraliste ainsi qu'aux petites espèces et moins aux carnivores strictes. Cependant, aucun effet lié à la stratégie r/K n'a été mise en évidence. De

plus, les aires protégées et zones naturelles ne sélectionnaient aucun trait spécifique, ce qui confirme leur rôle de refuge pour tous les mammifères.

Les méthodes utilisées pendant ma thèse sont particulièrement intéressantes car non invasives et ne dérangent pas les animaux, tout en permettant d'engager la discussion au sujet de la conservation des mammifères avec les acteurs locaux du territoire.

## **Discussion**

Grâce à des méthodes complémentaires, nous avons étudié la réponse des mammifères africains selon des gradients d'anthropisation pour évaluer leur anthropodépendance et leurs capacités à occuper les paysages anthropisés. Le paysage mosaïque actuel de la réserve de biosphère de la Garden Route semble propice au maintien des mammifères car nous avons mis en évidence une communauté complexe de 16 mammifères, témoignant de leurs diverses capacités d'adaptation aux habitats anthropisés et favorisé par certains traits d'histoire de vie. Les espèces dites synanthropiques seraient plutôt des carnivores avec un régime alimentaire flexible et de petites taille, comme la mangouste grise (*Herpestes pulverulentus*) restant discrètes pour utiliser les mêmes habitats que les humains alors que les espèces anthropophiles, comme le babouin ou le potamochère du Cap (*Potamochoerus larvatus*) seraient de plus grosses espèces, avec un régime plutôt omnivore ou herbivore et dépendraient du refuge des zones naturelles. Le réseau de végétation naturelle, soutenu par des initiatives individuelles, crée de la connectivité pour les mammifères entre les zones modifiées par les activités humaines et le parc national, ce qui est essentiel au maintien des mammifères dans les zones anthropisées et contribue au bien-être des populations humaines (Obura et al., 2021).

Les modèles et les méthodes utilisés nous ont permis de fournir des éléments et des outils pour aider à la gestion et à la prise de décision pour l'avenir de la biodiversité à l'échelle locale, dans lesquels les populations pourraient être impliquées autant par leurs connaissances que par leurs actions pour la mise en place de solutions durables de coexistence. Les résidents de la réserve de biosphère de la Garden Route sont à l'initiative de nombreux projets de conservation (e.g. <https://savewild.co.za/>) et se sont montrés prêts à s'impliquer au côté des chercheurs. Ils ont collaboré avec entrain à mon projet, ce qui ouvre la voie pour co-construire des nouveaux modèles de conservation efficaces et sur le long terme. La réserve de biosphère de la Garden Route offre un terrain d'expérimentation idéal pour concilier activités humaines durables et conservation de la biodiversité, et ainsi proposer des solutions locales à des problèmes mondiaux. L'Afrique est un continent d'avenir sur le plan social et économique, mais aussi pour la conservation, sujet sur lequel ils jouent d'ailleurs déjà un rôle majeur (Lindsey et

al., 2017). Je suis convaincue que les pays occidentaux ont beaucoup à apprendre pour développer des modes de coexistence avec les mammifères et notamment les grands carnivores. Il n'existe cependant pas de solution simple pour préserver la biodiversité dans un monde complexe et multi-acteurs, ni de solution universelle qui fonctionne à coup sûr (Ostrom, 2009), c'est pourquoi, la recherche doit être co-construite avec les acteurs et résidents du territoire afin d'élaborer des mesures de conservation justes et honnêtes qui bénéficieront aux populations et à la nature (McShane et al., 2011). Travailler pour aménager des espaces partagés adaptés aux humains et à la biodiversité est la première étape du processus de transformation pour atteindre l'objectif de « partage de la Terre » (Obura et al., 2021; Rosenzweig, 2003).

# List of abbreviations

AWT: Africa Wildlife Tracking

CALM: Collaborating Across the Landscape to Mitigate impacts of development

CBA: Critical Biodiversity Area

COP: Conference of the Parties

CT(s): camera trap(s)

GPS: Global Positioning System

GRBR: Garden Route Biosphere Reserve

GRDM: Garden Route District Municipality

GRNP: Garden Route National Park

IUCN: International Union for Conservation of Nature

LEK: Local Ecological Knowledge

MCH: Mitigation and Conservation Hierarchy framework

PA: Protected Areas

SA: South Africa

SANParks: South African National Parks

USA: United States of America



# List of publications and communications

## Scientific articles:

### Published

- **Alice Bernard**, Ana S.L. Rodrigues, Victor Cazalis, David Grémillet. Towards a global strategy for seabird tracking. *Conservation Letters*. 2021; 00:e12804. <https://doi.org/1111/conl.12804>
- **Alice Bernard**, Lizette Moolman, Melanie A. de Morney, Chloé Guerbois, Jan A. Venter, Hervé Fritz. Height related detection biases in camera trap surveys: insights for combining data sets. *Koedoe* 65, no 1 (2023): 5. <https://doi.org/10.4102/koedoe.v65i1.1734>
- David Grémillet, Aurore Ponchon, Pascal Provost, Amandine Gamble, Mouna Abed-Zahar, **Alice Bernard**, Nicolas Courbin, Grégoire Delavaud, Armel Deniau, Jérôme Fort, Keith C. Hamer, Ruth Jeavons, Jude V. Lane, Liam Langley, Jason Matthiopoulos, Timothée Poupert, Aurélien Prudor, Nia Stephens, Alice Trevail, Sarah Wanless, Stephen C. Votier, Jana W.E. Jeglinski. Strong Breeding Colony Fidelity in Northern Gannets Following High Pathogenicity Avian Influenza Virus (HPAIV) Outbreak. *Biological Conservation* 286 (2023): 110269. <https://doi.org/10.1016/j.biocon.2023.110269>.

### Submitted

- **Alice Bernard**, Hervé Fritz, Anne-Béatrice Dufour, Jan A. Venter and Chloé Guerbois. A local ecological knowledge-based assessment of anthropodependence for large mammals in anthropogenic landscapes. (*Biological conservation*)

### In preparation

- **Alice Bernard**, Lain E. Pardo, Lizette Moolman, Melanie A. de Morney, Chloé Guerbois, Jan A. Venter, Hervé Fritz. Spatio-temporal overlap between African mammals and humans in a multifunctional landscape: insights on the concept of anthropodependence.
- **Alice Bernard**, Chloé Guerbois, Jan A. Venter and Hervé Fritz. Comparing local ecological knowledge with camera trap data to study African mammals' occurrence in anthropogenic landscapes of the Garden Route Biosphere Reserve.

- **Alice Bernard**, Chloé Guerbois, Jan A. Venter and Hervé Fritz. Combining local ecological knowledge with camera traps to assess the link between African mammal life history traits and their use of anthropogenic landscapes.
- Elizabeth Kennedy-Overton, **Alice Bernard**, Pierre-Cyril Renaud, Grant Hall, Chloé Guerbois, Franck Prugnolle, Hervé Fritz and Virginie Rougeron. Impact of anthropization on chacma baboon (*Papio Ursinus*) diet in South Africa.

### **Oral communications**

- Towards a global strategy for seabird tracking. Alice Bernard, Ana S.L. Rodrigues, Victor Cazalis, David Grémillet. Colloque migration, France, 2020.
- A citizen-based quantitative assessment of anthropo-dependence for large mammals in anthropogenic landscapes. Alice Bernard, Jan A. Venter, Hervé Fritz, Chloé Guerbois, Garden Route Interface and Networking (GRIN) Meeting, 2022
- Combining methods to document the persistence of African mammals in anthropogenic landscapes, Alice Bernard, Jan A. Venter, Chloé Guerbois, Hervé Fritz, International Congress for Conservation Biology (ICCB), 23-27 July 2023, Rwanda.

### **Posters**

- Height related detection biases in camera trap surveys: insights for combining data from various sources. Alice Bernard, Lizette Moolman, Melanie A. de Mornay, Chloé Guerbois, Jan A. Venter, Hervé Fritz. Southern African Wildlife Management Association (SAWMA) Conference, 2021.
- The importance of Critical Biodiversity Areas in the mosaic landscape of the Garden Route. Alice Bernard, Lizette Moolman, Melanie A. de Mornay, Chloé Guerbois, Jan A. Venter, Hervé Fritz, Garden Route Interface Networking (GRIN) Meeting, 2022.

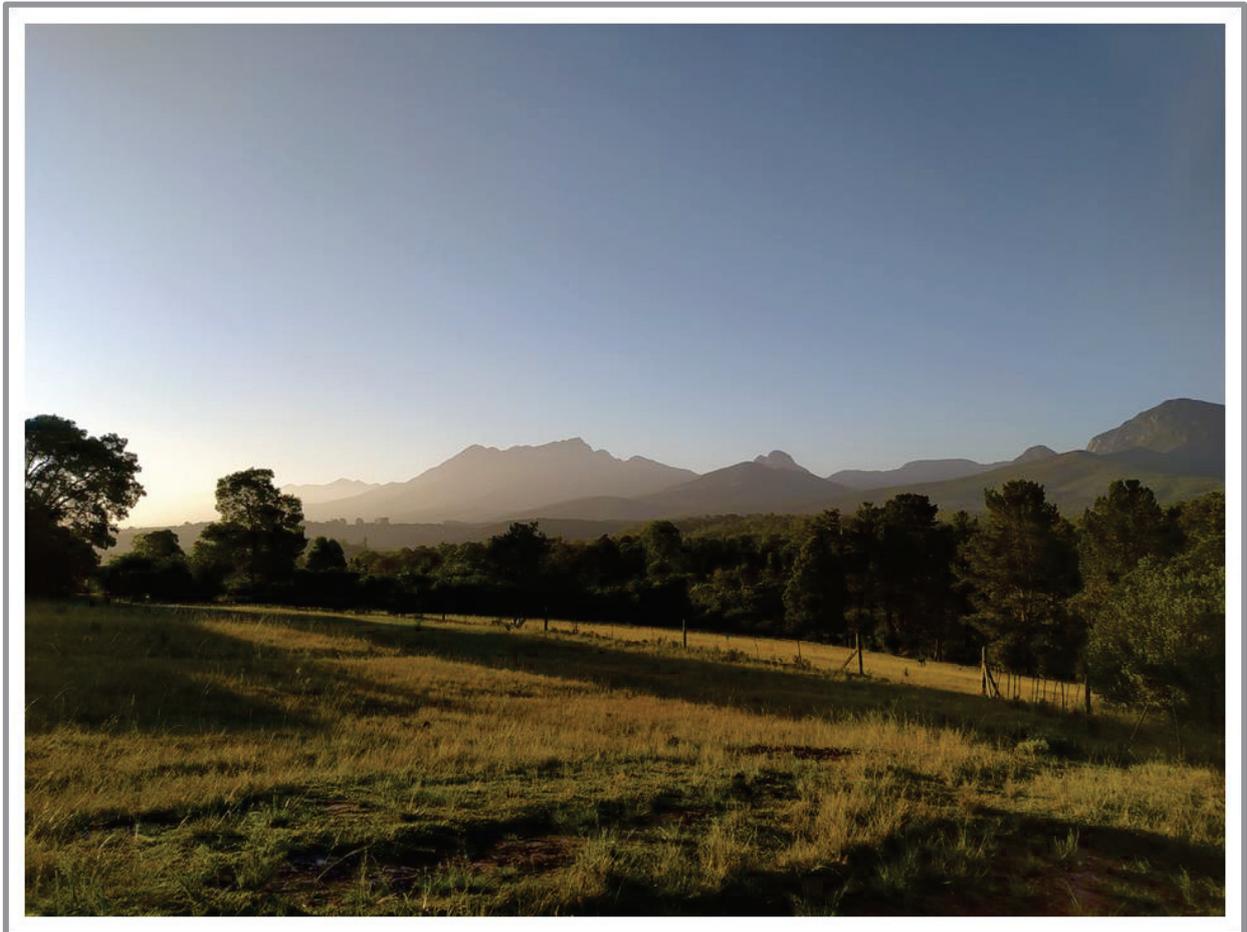
## Note to the reader

This manuscript is written in the form of a *PhD* thesis based on manuscripts, organized in three chapters. The manuscripts are structured around a general introduction, general materials and methods and a general discussion. Each chapter begins with detailing the objectives and main results of the section. The manuscripts are presented as if they were formatted for journals, although they are still in preparation. One is accepted, and another is submitted. There is some repetition because of the manuscript format of the thesis but this was unavoidable.

I started my *PhD* in December 2019, four months before the beginning of the COVID-19 pandemic, and was cut short by a potential full year of fieldwork. It was therefore not possible to achieve everything that was initially desired. Choices had to be made. While this has led to some disappointment on my side and impact on the final product, we did our best to answer the scientific questions of this *PhD*. I spent a total of 18 months in George, which gave me an incredible experience of meeting the residents, seeing and tracking the wildlife and immersing myself in the South Africa culture. The photographs between each section were taken by me during my stay at Nelson Mandela University, George, South Africa, unless stated otherwise.



# General introduction



*« C'est en connaissance de cause que nos ancêtres ont déstabilisé les écosystèmes et la Terre. Puisqu'il n'y a pas de passage de l'inconscience à la conscience, puisque le capitalisme financiarisé actuel fait bon ménage avec de nouvelles formes de désinhibition, tout porterait à craindre que les choses vont continuer comme avant. »*

*L'évènement Athropocène,*

*Christophe Bonneuil et Jean-Baptiste Fressoz*



# 1 | The Anthropocene

## 1.1 | A new geological era

Due to domestication, human settlement, the apparition of an agricultural lifestyle and more recently, the Industrial Revolution (Bonneuil & Frescoz 2016), the human population has increased drastically from 1 billion in 1804 to 8 billion in 2022 (Worldometers 2023). Simultaneously, the human ecological footprint, a measure of the cumulative impact of humans on the landscapes (e.g. presence of infrastructure, human-modified land cover), expanded as well (Crist et al. 2017). Between 1700 and 2000, most of the planet became modified by humans and their activities (Ellis et al. 2010). These transformations are rapidly occurring: the human footprint has increased by 9% between 1993 and 2009 (Venter et al. 2016b). The needs of humans, especially those for food demand, led to land conversion for agriculture, which is responsible for habitat loss, and the hunting of wildlife (Crist et al. 2017). The expansion of agriculture is leading to deforestation in many places across the world, and agricultural production for food, energy, and fabric is one of the major constraints to biodiversity protection (Foley et al. 2005; Crist et al. 2017). Croplands and pastures represented 40% of the planet's terrestrial surface in the 2000s, becoming the predominant biome (Foley et al. 2005). Nowadays, 58.4% of natural terrestrial land has been moderately to intensively disturbed by humans and their activities (Williams et al. 2020a). These modifications have diminished ecosystem resilience, *i.e.* the capacity to return to its initial state if it is disturbed, and their capacity to provide services at a level that is now threatening human well-being and societies (Foley et al. 2005; Folke et al. 2021). The most significant changes have occurred since the 1950s (Steffen et al. 2011). Human activities impacted many natural elements such as the greenhouse gas concentration, the ocean's acidity, the river systems and the nitrogen cycle, to cite a few. It led to modifications of original ecosystems and has created modified ones (Crutzen 2002), to the point where the impact of humans on nature and the ecosystems becomes equivalent to geological and environmental forces (Corlett 2015). The '*Anthropocene*' is the name given by researchers to this new geological era, which would have begun with the change in human activities during the industrial era, around the late 18<sup>e</sup> century (Crutzen 2002; Steffen et al. 2011). The name comes from the Greek '*ánthrōpos*' meaning '*human*' and '*kainos*', meaning '*recent, novel*' (Bonneuil & Frescoz 2016).

In the 2000s, humans were using 23.8% of the net productivity of the planet for their activity (Haberl et al. 2007). Resource appropriation and use have been and still are unequal between Northern and Southern hemisphere countries (Haberl et al. 2007; Folke et al. 2021). Colonial governments have externalized their ecological footprint by relying on the land and resources of their colonies for their economic development (Bonneuil & Frescoz 2016). They accessed a

larger quantity and quality of resources and often destroyed various of their colonies' ecosystems (Bonneuil & Fressoz 2016). To recall that the origin of the deregulation of the planet is based on an unequal use of ecological resources, the Anthropocene could be renamed '*Capitalocene*' (Bonneuil & Fressoz 2016). Western countries are indebted to Africa, America and Asia for their industrial development (Bonneuil & Fressoz 2016).

Humans play several significant roles in ecosystems (Moll et al. 2021). They are creating new niches by transforming natural systems into modified ones, e.g. urban areas and or have a pseudo-mutualist role by facilitating other species to live close to them, for instance, by putting nest boxes or bird feeders (Moll et al. 2021). Humans sometimes have a super predator action and are affecting 'keystone' species, *i.e.* which have outsized ecological impacts, such as lions (*Panthera leo*) or elephants (*Loxodonta* spp.), across different ecosystems (Worm & Paine 2016; Moll et al. 2021). Worm and Paine (2016) introduced the term '*hyperkeystone*' species, highlighting the major role humans play in an ecosystem and integrating them into the complex trophic interactions between species.

## 1.2 | A declining biodiversity

Destruction of natural habitats for agriculture, logging or development is the primary cause of species decline (Tilman et al. 2017). Around 9% of terrestrial species (representing 500,000 species) do not have enough habitat areas for their survival (IPBES 2019). Species are also affected by direct mortality, e.g. by hunting (Tilman et al. 2017; Harfoot et al. 2021). The rate of human exploitation of marine and terrestrial species is 15 times higher than the rate of any other predator on Earth (Worm 2015). Species which are not usually killed by other predators such as healthy adult prey, *i.e.* the reproductive capital of the populations or other predators, are more likely to be killed by human recreational hunting or industrial activities, such as fisheries (Darimont et al. 2015). The present hunting and fishing rates are not sustainable and incompatible with preserving biodiversity, which is why humans have been described as '*super predators*' (Darimont et al. 2015). Another threat is the presence of invasive species, which can have a considerable negative impact on indigenous species, such as feral cats (*Felis catus*), in Australia (Doherty et al. 2017). Finally, climate change, because it induces the rarity of food resources and water in certain areas, is threatening species by modifying their behavior and distribution (Tilman et al. 2017). For example, a survey on small mammal communities in Yosemite National Park in the United-States of America (USA), showed that low-elevation species migrated to a higher elevation in response to higher temperatures, whereas the ones in high-elevation areas contracted their home ranges (Moritz et al. 2008). Climate change constraints push various animals to look further and go to new areas to find resources (Mariki

et al. 2015; Pérez-Flores et al. 2021), which could lead to increased conflicts with humans over access to resources in the future (Abrahms et al. 2023). Because of indirect (demographic, economic, technological, governance or conflict) and direct (land use change, exploitation, climate change, pollution or invasive species) drivers, since 1970, the natural ecosystems have declined by 47% in comparison to their earliest state, and the biomass of wild mammals has been reduced by 82 % (Diaz 2019; IPBES 2019). The Living Planet Report pointed out that the wild vertebrate population decreased by 69% since 1970 (WWF 2022). According to Hill et al. (2018), 75% of the loss of species abundance and richness happened after the 1800s (Hill et al. 2018). Africa is facing the most drastic decline (Hill et al. 2018). Globally, while the biomass of humans and their livestock multiplied by four, the biomass of marine and terrestrial wild mammals divided by six (Bar-On et al. 2018). The global biomass of mammals and birds is largely represented by humans and their domestic animals (livestock, poultry, domestic birds, and pets) which account for 95% of the biomass, while the biomass of wild mammals and birds is only 5% (Bar-On et al. 2018). The present rate of species extinction is 1000 times higher than the geological average (Pimm et al. 2014). Between 1970 and 2004, animal population abundance showed a global decline, with Latin American and African regions facing the largest losses (-95% and -66% respectively) (WWF 2022). The number of threatened species is expected to increase by 7% by 2020 and 14 % by 2050, with human population growth (McKee et al. 2004). The Red List (IUCN 2022), the Living Planet Index (Loh et al. 2005) and the Global Assessment Report on Biodiversity and Ecosystem Services (IPBES 2019), are regularly updated to give the pulse of worldwide biodiversity (Godet & Devictor 2018). Land being a limiting resource for both humans and nature, Tilman et al. (2017) proactively recommended that international entities limit habitat destruction and fragmentation, and protect natural land to reduce the induced extinction risk for biodiversity. These must also be linked to a change in diet (reducing the consumption of animal products and sugar), especially for rich countries, and a transition towards local agricultural production. Researcher's opinions are unanimous and continuing as humans have done over the past decades is not sustainable for the future (Bonneuil & Fresco 2016; Folke et al. 2021).

## 2 | From protected areas to shared Earth

### 2.1 | History of conservation and protected areas

The first European explorers who arrived in southern Africa discovered an abundance of wildlife that they killed, consumed and sold, leading to their significant decline (Rodary 2019). At the turn of the 20<sup>th</sup> century, to counterbalance the decline of animal populations, hunters and colonial administrators limited hunting seasons and restricted the number of individuals and species to kill (Carruthers 2017). Hunting was exclusively allowed for the elite and forbidden to local populations and most settlers (Rodary 2019). However, these measures were insufficient to counterbalance the losses (Rodary 2019). In South Africa, private owners erected fences to prevent people from hunting on their properties and enclosing wildlife (Carruthers 2017). The first game reserves with conservation purposes appeared by 1900 (Carruthers 2017). Because only some species were protected, these reserves played a heterogeneous role in mammal conservation (Carruthers 2017). For example, large carnivores such as cheetahs (*Acinonyx jubatus*) or lions, considered as vermin, were encouraged to be killed. At the end of the 19<sup>th</sup> century, the idea of preserving untouched and protected nature for people's enjoyment appeared, and Yellowstone, in the USA, was the first national park established in 1872 (Phillips 2004). This was followed by many countries across the world (Phillips 2004). Protected areas were often created to preserve virgin space, untouched by any human activity (Blanc 2020). Royal Natal National Park was the first national park in South Africa and was established in 1906 by the British Government, but only recognized in 1926, the year that Kruger National Park was established (Carruthers 2017). Protected areas in Africa are the relic of colonial history and were dedicated to recreational tourism (Carruthers 2017; Rodary 2019). It has often led to the eviction of human populations living there and was frequently imposed on local communities (Bourgeois et al. 2023), whereas protected areas should be for and designed by local people (Blanc 2020). Conservation efforts mostly focused on the protection of large mammals, especially the big five (elephant, rhinoceros (*Ceratotherium* spp.), buffalo (*Syncerus* spp.), lion and leopard (*Panthera pardus*)), and spatial segregation between human populations and natural spaces has emerged (Rodary 2019). Since the 2000s, ecological alerts and mobilization have become increasingly important and were supported by the various Intergovernmental Panel on Climate Change reports warning about global warming and environmental degradation (Bonneuil & Fressoz 2016).

Despite the end of the colonial period, the Western conception of nature conservation remained (Bourgeois et al. 2023). The concept of decolonization of conservation appeared at the end of the 20<sup>th</sup> century, encouraging an approach that included the values of local communities and recognized the importance of the surroundings of protected areas for

conservation (Trisos et al. 2021; Bourgeois et al. 2023). Today, ecology still needs to be decolonized. Trisos et al. (2021) suggested practices to this end: 1) decolonizing people's minds by opening them to other ways of carrying out and communicating science, 2) knowing human history, 3) decolonizing the access to science, 4) decolonizing access by including new expertise and local knowledge and 5) building inclusive and diverse teams to develop, deconstruct and provide new knowledge.

## 2.2 | Conservation and protected areas

### 2.2.1 | Conservation

Conservation biology emerged at the end of the 1970s and focuses on the problems faced by species, communities and their ecosystems (Soulé 1985). It is a multidisciplinary science, that aims to improve human well-being and protect biodiversity through environmental management (Soulé 1985; Kareiva & Marvier 2012). The approach is holistic, aiming to protect entire communities and ecosystems by assessing the status of the biodiversity, evaluating the threats and proposing solutions to conserve biodiversity (Soulé 1985; Godet & Devictor 2018). Conservation biologists often have to give advice and recommendations to governments and private organizations (Soulé 1985). Actions are broad and can be implemented locally or globally (Godet & Devictor 2018). Mace et al. (2014) described the shift of conservation perception over the last decades. Before the 1960s, the approach was focused on protecting '*nature for itself*', to preserve nature from humans in untouched natural habitats. Human and nature were considered as separate. This worked through management of protected areas based on species conservation and remains one of the dominant approaches nowadays. Between the 1970s and the 1980s, the conservation focus shifted to '*nature despite people*', where the main goal became to protect species and nature from human-induced threats. Conservation in the 21<sup>st</sup> century started to include ecosystems as providers of vital services. This led to the concept of '*nature for people*'. Since the 2010s and still today, the place of humans has been reintegrated as a part of nature, and conservation now considers the link between '*people and nature*', as a complex relationship. These four practices and approaches are still in place (Mace 2014). Williams et al. (2020b) examined whether conservation science was effectively saving biodiversity, and observed that most publications focus on describing the state of nature and not on testing the implementation of conservation measures. Substantial progress could be made by applying research results and implementing measures on the ground (Williams et al. 2020b).

### 2.2.2 | Protected areas

According to the International Union for Conservation of Nature (IUCN) definition, 'A *protected area* is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values'. Protected areas increased from 10,000 in 1960 to 177,547 in 2010 (12.7% of land surface and islands). In 2021, 15.8% of the planet's land surface was protected, and was separated into 267,085 protected areas (UNEP-WCMC et al. 2020). They play a major role in protecting natural habitats, such as forests, but their effectiveness in protecting species populations is often less conclusive, although in most cases positive, because of the high level of threats frequently bordering protected areas (Geldmann et al. 2013). Protected areas have been shown to be globally effective for the conservation of medium to large-bodied mammals (Chen et al. 2022). However, the effectiveness of protection can substantially vary between areas and does not necessarily protect suitable habitat for all species within an area (Cazalis et al. 2020; Maxwell et al. 2020). Between 1970 and 2005, African mammal populations declined by an overall average of 59% (Craigie et al. 2010). Heterogeneous variations were visible among regions, with western Africa facing the largest decline (Craigie et al. 2010; Scholte et al. 2021). The severity of the threats to wildlife were best described by geographic and socio-economic variables (Lindsey et al. 2017b). Governments are confronting food scarcity, insecurity, poverty and the need to protect their abundant and threatened wildlife (Scholte et al. 2021). The funds allocated to protected areas are often too small compared to the work that needs to be done (Scholte et al. 2021; Appleton et al. 2022). One other issue is the lack of human resources necessary to run such conservation measures (Scholte et al. 2021; Appleton et al. 2022). Protected areas mitigate the negative impact of human-induced threats to mammals, which would be more drastic without them (Craigie et al. 2010). Geldman et al. (2019) suggested that part of the ineffectiveness of protected areas would be because of their rapid growth to fit biodiversity targets, but without giving them the proper tools to be effective. Furthermore, Rodrigues et al. (2004) highlighted that the global network of protected areas did not represent all species. Indeed, preserving low-density species with large home ranges at a small scale is probably impossible (Rosenzweig 2003). To be more effective, protected areas need to be connected to allow animal movement (Brennan et al. 2022). Several important areas crucial for animal movement remain unprotected highlighting a lack of connectivity (Brennan et al. 2022). Protected areas are essential for preserving biodiversity but surrounding areas should also not be neglected and should be designed to improve their use by wildlife (Martin et al. 2016), which is the essence of transboundary conservation areas (Hanks 2003).

### 2.2.3 | The objectives of the COP15

The Rio Summit took place in 1992, to discuss fundamental questions relative to the planet's future (Locke et al. 2021). The United Nations Conference on Environment and Development created three conventions: the Convention on Climate Change, the Convention to Combat Desertification and the Convention on Biological Diversity (CBD) to conserve biodiversity and promote its sustainable use (Locke et al. 2021). The 15<sup>th</sup> Conference of the Parties (COP15) of the CBD was held between 196 countries in December 2022 in Montréal, Canada, and co-organized with China, to discuss the fate of biodiversity. Before it happened, the meeting raised some concerns. With Africa facing particularly important trade-offs between biodiversity protection and poverty reduction, many researchers were worried about how the measures would be implemented (Obura et al. 2021). Some researchers doubted that only increasing the surface of protected areas would be enough to preserve biodiversity and emphasized the need to effectively manage these protected areas (Scholte et al. 2022). The money invested in nature conservation is generally too limited to properly ensure protection, raising further concerns for implementing future objectives (Appleton et al. 2022). The COP15 resulted in four goals and 23 targets, such as the protection of 30% of the world's land and sea has to be reached by 2030, and 30% of degraded ecosystems need to be restored (Convention on Biological Diversity 2022). Another target was that money would be mobilized: developed countries would give \$200 billion of national and international funding for biodiversity as well as find \$20 billion each year by 2025 and \$30 billion per year by 2030 as financial support to developing countries (Convention on Biological Diversity 2022). The first goal was to reach natural ecosystem integrity, resilience and connectivity, stop human-induced extinction of species, maintain genetic diversity and increase populations of native species by 2050 (Convention on Biological Diversity 2022). The second one was to sustainably use biodiversity, with specific regard to the position of humans in conservation (Convention on Biological Diversity 2022). The third objective was about the equitable and sustainable use of genetic resources. The last goal aimed to correctly implement the objectives agreed upon during the COP15, particularly through adapted funding (Convention on Biological Diversity 2022).

## 2.3 | From 'nature for itself' to 'nature and people'

### 2.3.1 | The land-sparing/land-sharing debate and multi-functional landscapes

In many areas, the alteration of landscapes, especially through agriculture, has led to a homogenization to facilitate productivity and thus increase yields (Campbell et al. 2017). The land-sparing/land-sharing debate interrogates the best strategy to conciliate food production and conservation effort (Green et al. 2005). The land sparing strategy is to protect some natural land, and in parallel, do intensive agriculture (Green et al. 2005). Land-sharing aims at using

more extensive agricultural systems to maintain biodiversity in agricultural lands, thus having less land dedicated to conservation (Green et al. 2005). The land-sparing strategy often goes with the idea of intensive agriculture, which leaves no spaces for biodiversity (Wright et al. 2012). These land-use intensifications appeared to homogenize species assemblages and decrease the resilience of an ecosystem (Newbold et al. 2018; Folke et al. 2021). This approach is increasingly being debated. Land-sparing seems to be the best strategy to meet the demand for food while conserving biodiversity in some countries (Phalan et al. 2011), whereas others suggest that low-impact agricultural landscapes, contrary to intensive ones, may manage to maintain a sustainable habitat for some species (Lovell & Johnston 2009). Heterogeneous landscapes are reported to be more resilient and less vulnerable to disease or the effects of climate change (Lovell & Johnston 2009). The land-sharing strategy might play a major conservation role for threatened bird species in these landscapes (Wright et al. 2012). Furthermore, even if their densities were lower than in protected areas, carnivores were found using agricultural matrices in South Africa (Ramesh & Downs 2013; Ramesh et al. 2017; Faure et al. 2021).

According to Fahrig et al. (2022), protecting several small natural habitat patches would be more efficient than one single large one. Single large protected areas would only be more effective when the movement between patches, risk spreading and the heterogeneity across habitats were low (Fahrig et al. 2022). This suggests the value of increasing the number of natural habitat patches in human-modified habitats for conservation purposes. Researchers are considering new approaches for conservation, such as multifunctional landscapes, which would provide environmental, social and economic functions (Reyers et al. 2012). These landscapes combine advantages and maintain ecosystem services, which are the benefits to humans produced by the ecosystem such as pollination, clean water or food production (Reyers et al. 2012). They are crucial for food security, maintenance of biodiversity and ecological functions, but could also contribute to population's well-being through the support of cultural and recreational needs (Jones-Walters 2008; O'Farrell & Anderson 2010). They usually provide more diverse ecosystem services and positively impact more people than nonfunctional ones, which tend to disconnect people from nature (Fischer et al. 2017). However, these landscapes bring together many stakeholders, making them difficult to manage, as their needs and opinions may differ (Fischer et al. 2017). Implementating sustainable multifunctional landscapes needs transdisciplinary approaches, considering social, ecological, and economic criteria for land planning and including exchanges with stakeholders (Lovell & Johnston 2009; O'Farrell & Anderson 2010). Ecosystems are undoubtedly being transformed by humans, which modified their original characteristics, so should be the way of doing conservation (Hobbs et al. 2009). Multifunctional landscapes could

improve sustainability and play a role in conservation, while also improving people's well-being (Reyers et al. 2012; Fagerholm et al. 2020). Mosaic landscapes with natural and managed green spaces are important for the persistence of several vertebrate species in the global South, especially South Africa (Downs et al. 2021). The Durban Metropolitan Open Space System (D'MOSS) has natural and managed greenspaces linked through planning to allow connectivity and persistence of species (Roberts 1994).

### 2.3.2 | '*Shared Earth*' and large scale conservation areas

Obura et al. (2021) called for a shift to a '*shared Earth*' approach, to reconnect biodiversity and people. The purpose of these shared areas is to connect people and nature by designing more wildlife-friendly habitats to complement protected areas. Finding solutions to share human-dominated environments with wild species, by redesigning semi-natural to urban areas, is what is prone by '*reconciliation ecology*' (Rosenzweig 2003). The aim is to provide more suitable space for species, to slow down biodiversity collapse (Rosenzweig 2003). Some modifications of human-modified habitats could increase their use by wildlife (Rosenzweig 2003). For example, increasing connectivity between natural habitats seemed to improve species richness in urban nature reserves (Roberts 1994; McPherson et al. 2016; Maseko et al. 2020; Zungu et al. 2020a, 2020b; Schnetler et al. 2021). Allowing undergrowth vegetation within oil palm plantations and maintaining corridors increased the probability of occurrence of mammal species in Columbia (Pardo et al. 2019). Wildlife-friendly areas are essential for the persistence of mammals in human-dominated mosaic landscapes, as they provide connectivity across these landscapes and link them to natural green space (protected areas) and managed green species (Roberts 1994; McPherson et al. 2016; Maseko et al. 2020; Zungu et al. 2020a, 2020b; Obura et al. 2021). Shared landscapes complement protected areas, thus increasing the areas suitable for wildlife, which is particularly important for species with large home ranges, such as carnivores (Carter & Linnell 2016; Streicher et al. 2020, 2021; Obura et al. 2021).

Biosphere reserves and transboundary conservation areas are governance models that appeared respectively in the 1970s and 1990s, and use transdisciplinary approaches to promote sustainable socio-economic development while protecting biodiversity (Batisse 1982; Hanks 2003; Pool-Stanvliet & Coetzer 2020). They could be considered as '*shared Earth*' models, as they promote the development of suitable areas for wildlife outside protected areas. They encourage studying the interactions between social and ecological systems in areas that encompass protected areas and their surroundings (Pool-Stanvliet & Coetzer 2020; Bourgeois et al. 2023).

## 3 | The impact of human activities on mammals

### 3.1 | Deleterious effects

Moving outside protected areas can represent a risk of human-induced mortality (van der Meer et al. 2014). Bateman & Fleming (2012) showed that road collisions were the first cause of death for carnivores in the USA, followed by hunting, pollution, poisoning and disease. Humans play a major role in ecosystem dynamics and affect the spatial and temporal habits of animals, leading to modification of their trophic interactions (Darimont et al. 2015; Sévêque et al. 2020; Moll et al. 2021). These modifications often negatively affect wildlife but some species can adapt and benefit from the new conditions provided by humans (Bateman & Fleming 2012; Hulme-Beaman et al. 2016; Moll et al. 2021).

#### 3.1.1 | Modification of the spatial niche

Human-modified landscapes often change species' spatial niche, pushing them to use other environments (Box 1, Figure 1) (Sévêque et al. 2020; Van Scoyoc et al. 2023). However, some vertebrate species successfully persist in these mosaic landscapes (Widdows & Downs 2015, 2017; Patterson et al. 2017, 2018, 2019; Streicher et al. 2020, 2021). The term '*anthropogenic resistance*' has been introduced to describe the impact of human behavior on species movement, which might impact biophysical or functional connectivity (Ghoddousi et al. 2021). Separation of human properties and wildlife with fences, which is common to protect crops or livestock, thus reducing conflictual interactions, can negatively impact wildlife movement and isolate populations (Woodroffe et al. 2014). Human activities influence the distance travelled and home ranges of many species, e.g. birds, mammals, reptiles, amphibians, fish and arthropods (Doherty et al. 2021). Tucker et al. (2018) found that the movement of mammals in areas with higher human footprint was reduced from a half to a third compared to areas with a lower human footprint. High human footprint areas also tend to exclude species with large home ranges (Tucker et al. 2018). Reduction of movement is not without consequences as it can affect individual fitness, population viability as well as ecosystem processes such as predator-prey interactions or disease transmission (Tucker et al. 2018). Habitat fragmentation because of human modification can disconnect the patches of natural habitat (Fischer & Lindenmayer 2007). The resulting sparse and small fragments of natural habitats create new interfaces between domestic and wild animals, where they may interact. Predation of domestic dogs (*Canis lupus familiaris*) and cats on wildlife has been documented, which could lead to modifications of the trophic guild, as they represent competition or risk of predation (Paschoal et al. 2012; Doherty et al. 2017; Carricondo-Sanchez et al. 2019; Seymour et al. 2020).

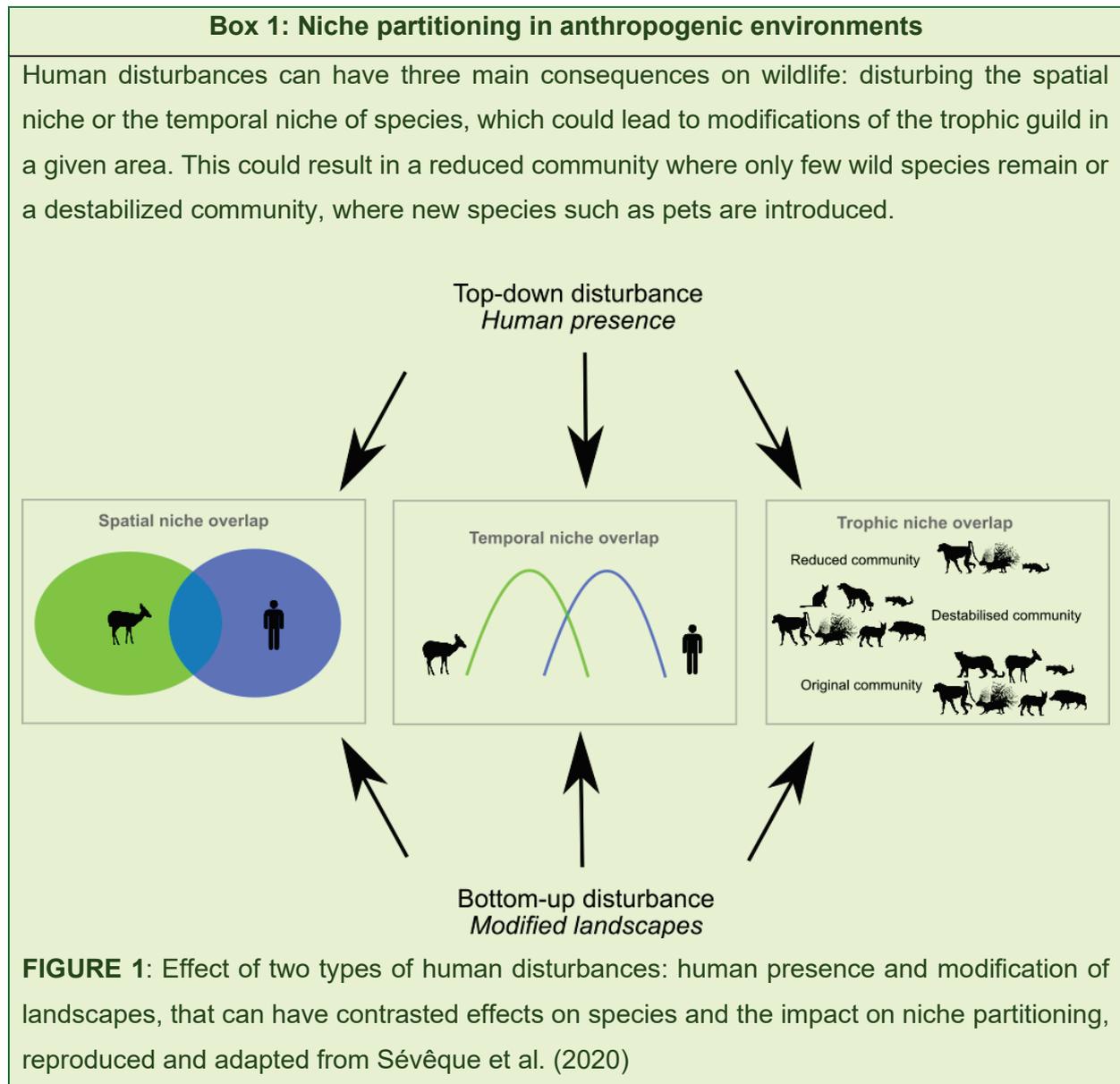
### 3.1.2 | Modification of the temporal niche

Human activities modify species' temporal niche (Box 1, Figure 1) (Gaynor et al. 2018; Van Scoyoc et al. 2023). Despite the fact that 70% of mammals are nocturnal (Cox et al. 2021), worldwide human activities can affect the temporal activity of species in response to recreation, temperature, light pollution or habitat change (Gaynor et al. 2018; Gilbert et al. 2022a). A shift to nocturnality can reduce conflicts with humans, but also induce dietary modifications to nocturnal prey (Gaynor et al. 2018). The shift can also lead to mismatches with diurnal adaptation such as an incorrect retinal structure or inappropriate circadian clock, difficulties of intraspecific interaction (e.g. finding mates), or increasing interspecific interactions (e.g. competition or predation), which can respectively have an impact at the individual, the population or the community level (Gaynor et al. 2018; Levy et al. 2019). The fitness of a species can therefore decrease with a change in its temporal activity (Gilbert et al. 2022a). The permanent light in urban areas can also alter species movement and nocturnality if perceived as a risk, affecting predator-prey interactions (Dominoni et al. 2016; Gaynor et al. 2018; Ditmer et al. 2021).

### 3.1.3 | Modification of the trophic interactions

Each species has a specific and defined position and role in an ecosystem resulting in complex trophic systems (Montgomery et al. 2019). Apex predators have a critical role in these trophic relationships (Montgomery et al. 2019; Burgos et al. 2023). They often exert pressure on prey populations, omnivores and mesocarnivores (Maxwell et al. 2020). Even in sparsely human-populated areas, the distribution of species can be modified, which could create an unbalance in guild relationships (Barbar et al. 2015; Mills et al. 2019). Human disturbance and habitat transformation, can modify dominance in guilds and associated trophic cascades by affecting the ecosystem suitability for some species. They induce a new dynamic landscape of fear for species, defined as the spatio-temporal perception of risk (predator, human) by a species, which can vary in space and time (Palmer et al. 2023). For example, human development and activities alter predator communities by affecting the presence of apex predators (Wang et al. 2015). Dominance in guilds could exacerbate the effect of human-altered habitats by increasing the presence of one species to the detriment of others, which can in some cases disappear from the area (Grimm et al. 2008; Sévêque et al. 2020). By changing predator-prey interactions, humans are unbalancing the landscape of fear in which species are occurring (Palmer et al. 2023). Communities occurring in anthropogenic contexts are either reduced (few species persisting) or destabilized, with the success of few species and the apparition of new domestic pets such as cats and dogs (Box 1, Figure 1) (Newbold et al. 2018; Sévêque et al. 2020). Every species is connected in an ecosystem, and a slight modification can unbalance

the whole system (Worm & Paine 2016; Palmer et al. 2022). Humans are now a part of it, and can impact community structure and trophic interactions (Worm & Paine 2016; Palmer et al. 2022).



### 3.2 | Positive impacts

Despite the negative impact of human-dominated landscapes and human activities, some wild species can be found in the vicinity of humans and even thrive in human-modified habitats. The endangered southern brown bandicoot (*Isodon obesulus obesulus*) in Australia successfully uses peri-urban areas, highlighting the potential that these environments could play in protecting threatened species (Maclagan et al. 2018). Commensal species such as rodents are often concentrated in human-dominated landscapes, e.g. in farmland or cities

(Pocock et al. 2004). Commensalism is defined as a relationship where one of the species benefits from the other, without impacting the other species (Hulme-Beaman et al. 2016). If some species can manage to live close to humans, this is because anthropogenic landscapes can offer new exploitable opportunities (Pocock et al. 2004; Fleming & Bateman 2018). Human-dominated areas for example, provide new food resources which may be used by species, from rubbish or crops (Fleming & Bateman 2018; Jansen van Vuuren et al. 2022; Mazue et al. 2023). Fleming and Bateman (2018) described novel predation opportunities that can be used by predators in anthropogenic landscapes, such as the presence of a new range of prey like livestock or pets (Braczkowski et al. 2012b; Treves & Bruskotter 2014). A study on caracals (*Caracal caracal*) showed that they changed their diets in urbanized contexts, and ate domestic cats (Braczkowski et al. 2012a). Anthropogenic areas can attract or concentrate prey around artificial lighting, waterholes, houses or in farming areas (Stenseth et al. 2003; Fleming & Bateman 2018). For non-carnivore species, human-dominated areas also offer constant food supplies with low variability that serve as predictable food sources to some species (Hulme-Beaman et al. 2016). African small antelopes supplement their diet by eating crops in the Overberg region of South Africa (Jansen van Vuuren et al. 2022). In the Cape Peninsula of South Africa, population growth as well as urban and rural transformation pushed chacma baboons (*Papio ursinus*) into marginal natural habitats while allowing them to benefit from food resources in human-modified habitats which are easy to access and predictable (Hoffman & O’Riain 2012). Anthropogenic environments could also enable new hunting strategies such as taking advantage of noise that distracts prey or on the contrary, indicating the presence of livestock (Loveridge et al. 2017; Fleming & Bateman 2018). Fences can reduce predators hunting effort by preventing prey from escaping (Woodroffe et al. 2014; Fleming & Bateman 2018). On the other hand, as apex predators often avoid humans and their habitats, contrary to smaller carnivores, human-dominated habitats could offer refugia for prey and smaller carnivores, thus reducing their risk of predation (Wang et al. 2015; Fleming & Bateman 2018; Gaynor et al. 2018). In Yellowstone National Park, USA, ungulates often stay in recreational areas, close to humans to use them as shields against predators (Berger 2007). Hulme-Beaman et al. (2016) proposed a framework to define wild species ability to live in anthropogenic environments, as they have a variety of possible responses. They separated species into four groups, according to their home-range overlap and diet overlap with anthropogenic habitats and resources: anthropophilic, synanthropic, anthropophobic and commensal or anthrodependent species (Box 2).

**Box 2: Species in anthropogenic environments: anthrodependence populations***Species without home-range overlap*

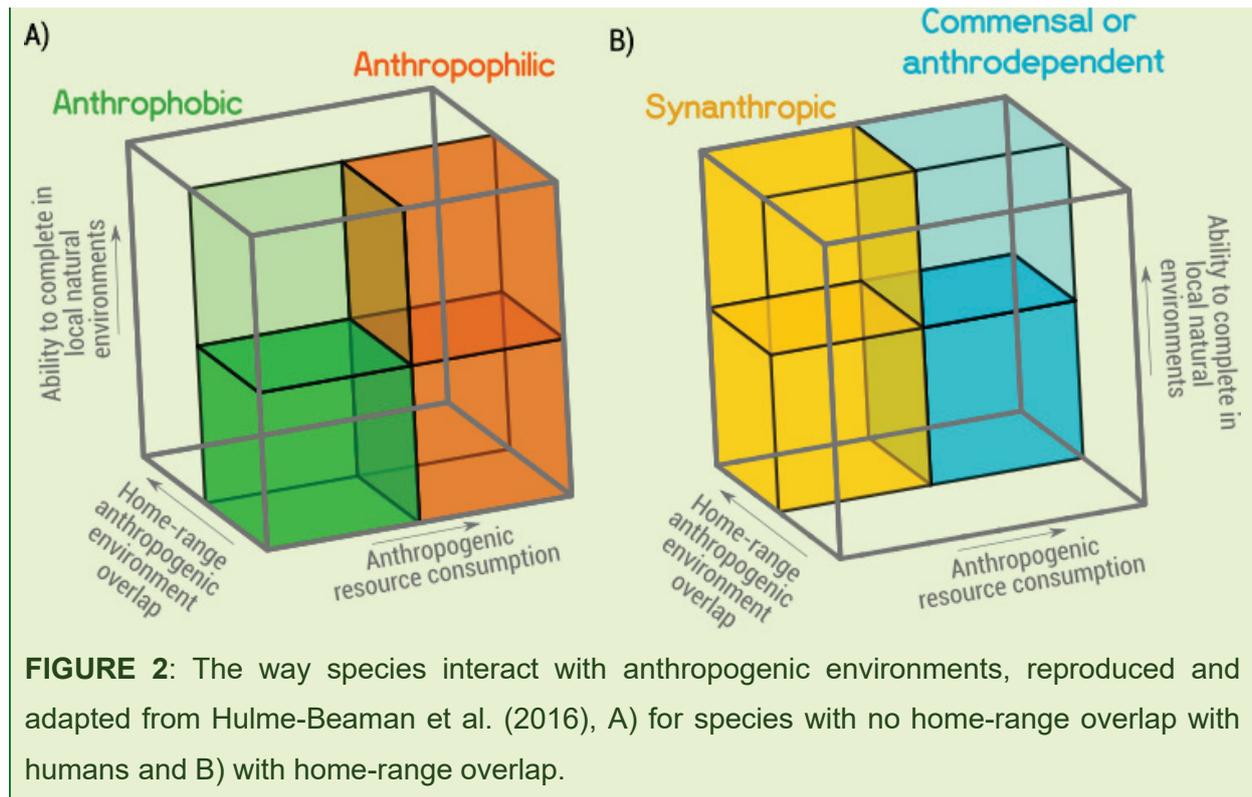
**Anthropophilic populations** (from the Greek '*ánthrôpos*' meaning '*human*' and '*phílos*' meaning '*who love*') are attracted to anthropogenic resources that they consume regularly but they do not use human habitats (in orange).

**Anthropophobic populations** (from the Greek '*ánthrôpos*' meaning '*human*' and '*phóbos*' meaning '*fear*') avoid humans, *i.e.* that there is no home-range overlap with humans and they do not consume human resources (in green). The light green cube represents species with a specialist diet, dependent on natural environments for natural food resources, whereas the darker green cube represents generalist species.

*Species with home-range overlap*

**Synanthropic populations** (from the Greek '*sùn*' meaning '*together*' and '*ánthrôpos*' meaning '*human*') have home ranges that overlap with anthropogenic environments but do not consume anthropogenic resources (in yellow).

**Commensal populations** (from the Latin '*con*' meaning '*with*' and '*mensalis*' meaning '*table*') consume human food resources and use human habitats (in blue). The light blue cube represents **commensal populations** able to use natural environments. The dark cube represents **obligate commensal populations**, *i.e.* populations entirely dependent on anthropogenic environments. Due to the dependence on human resources by some wild animals, which in addition a frequent impact on humans, the definition of commensal species may be inaccurate in an anthropogenic context. Hulme-beaman et al. (2016) developed a new term to name commensal populations that are associated with a dependence to anthropogenic resource: the **anthrodependent populations**. Because of the meaning of '*ánthrôpos*' and to be consistent with the terms anthropophilic and anthropophobic we will refer in this *PhD* thesis to '*anthropodependent*' populations.



**FIGURE 2:** The way species interact with anthropogenic environments, reproduced and adapted from Hulme-Beaman et al. (2016), A) for species with no home-range overlap with humans and B) with home-range overlap.

### 3.3 | Mammal adaptations

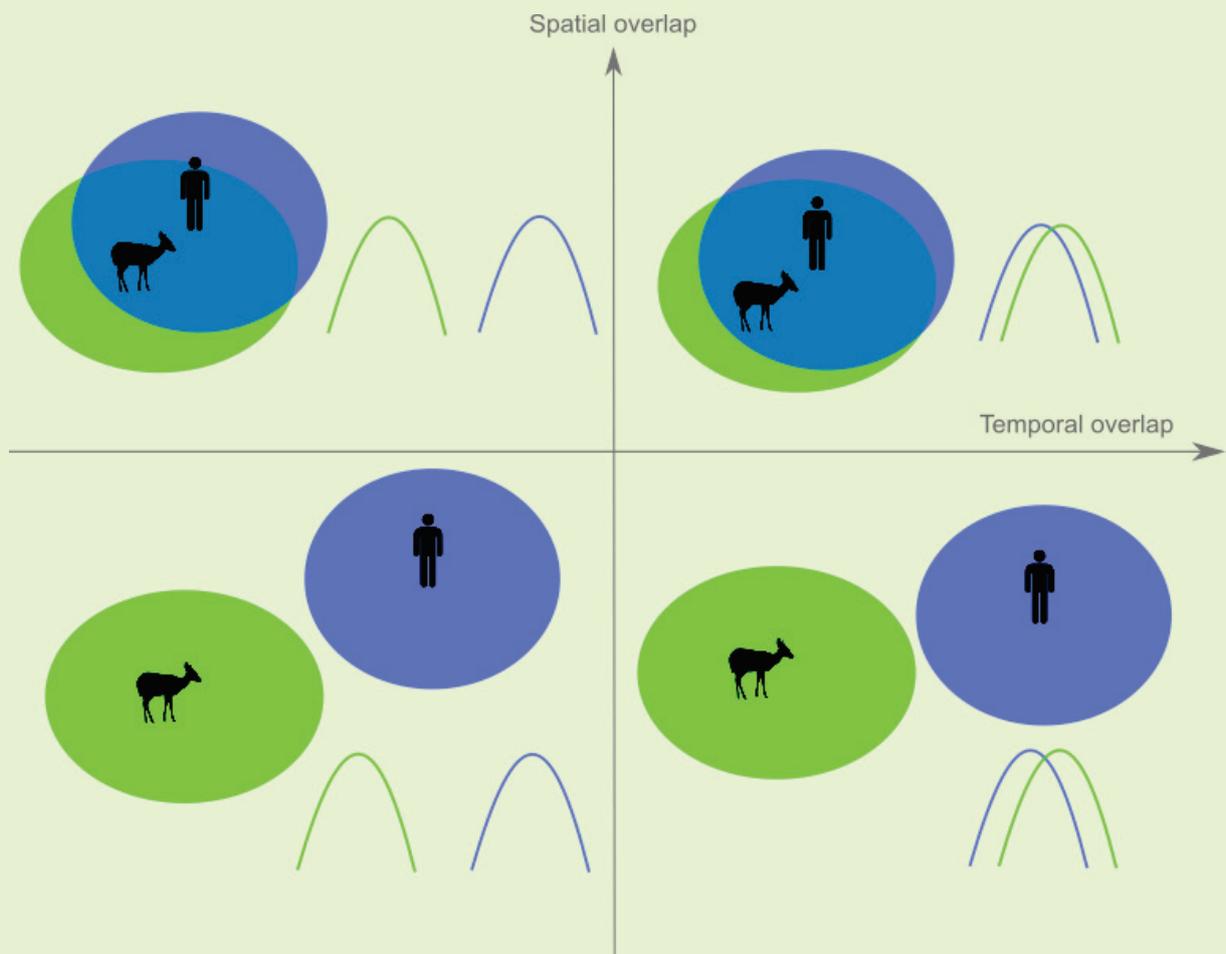
To live close to humans, wild species need to adapt to or avoid the new conditions created by humans (Brockie et al. 2009; Woodroffe et al. 2014; Moll et al. 2021). Another option is to be opportunist by using human facilities which is the case for anthropophilic, synanthropic and anthropodependent species (Figure 2). As presented previously, species can adapt to anthropogenic landscapes through spatial adjustments, *i.e.* not using the same habitats, or temporal adjustments, *i.e.* being active when humans are not (Boxes and figures 1, 2 and 3) (Gaynor et al. 2018; Frey et al. 2020; Sévêque et al. 2020). Caracal (*Caracal caracal*), forage in urban areas in South Africa, despite higher risk of collision, exposure to pollutants and diseases, but remain cryptic to mitigate the risk of being detected (Leighton et al. 2022b). Adaptations and selection through evolution require flexibility in species' ecological requirements and behavior (Santini et al. 2019; Schell et al. 2021), which might be possible because of specific life-history traits (Cox et al. 2021). Using anthropogenic landscapes can be worthwhile because wildlife can take advantage of the easy access and predictable resources available, which requires dietary flexibility (Bateman & Fleming 2012; Hulme-Beaman et al. 2016; Barrett et al. 2019). However, this could lead to competition and conflict with humans (Braczkowski et al. 2012a; Hoffman & O'Riain 2012; Yirga et al. 2012; Treves & Bruskotter 2014). The risk of persecution might be reduced by avoiding direct human encounter (Gaynor et al. 2018). Herbivores species can also use anthropogenic areas because

of the absence of predators, *i.e.* spatial niche partitioning (Berger 2007; Van Scoyoc et al. 2023).

Life history traits seem to play a major role in the extinction risk of some species when interacting with human-induced threats: the extinction risk of carnivores would be explained by species traits at 80% in areas with high exposure to humans, against only 45% in quieter places (Cardillo et al. 2004). In KwaZulu-Natal, the extinction vulnerability of mammals was linked to species body mass, trophic level, sociality and niche breadth (Zungu et al. 2020a). Studies have assessed which life history traits allow species to live in anthropogenic environments (Bateman & Fleming 2012; Santini et al. 2019; Suraci et al. 2021). The traits of adaptable species are often considered to belong to the r-strategy (high fecundity, large litter size). Species with plasticity in feeding behavior, diet (generalist or omnivorous habits) or habitats they occupy are also more likely to benefit from these new environments (Hulme-Beaman et al. 2016). Conversely, species with high space requirements, *i.e.* those most negatively impacted by habitat loss and fragmentation, are expected to not adapt well (Tucker et al. 2018). Solitary species, *i.e.* those that cannot live at high density and are often sensitive to interference, are unlikely to perform well in anthropogenic environments (Hulme-Beaman et al. 2016). However, Athreya et al. (2013) have shown that leopards (*Panthera pardus*) adapted to the proximity of humans, suggesting that some variability among species depends on factors other than life history traits. Furthermore, the traits of diurnal and nocturnal species are different (Cox et al. 2021). Species that are able to adapt seem to also possess greater cognitive abilities like neophilia, boldness, memory or social learning (Gil & Brumm 2014; Barrett et al. 2019), enabling them to make use of human environments. Predators, mainly because they have a high level of behavioral plasticity, could adapt and take advantage of opportunities that can be found close to human habitats (Barrett et al. 2019). Urban coyotes (*Canis latrans*) in North Carolina, USA, tended to be bolder and to be more attracted by human artefacts, than their rural counterparts, probably because of selection of such behavior (Brooks et al. 2020). On the opposite hand, some species may not be able to adapt because they do not have the required traits. This includes specialist species that depend on a specific resource or habitat to survive (Hulme-Beaman et al. 2016). These species are classified as anthropophobic (Box 2). They may be sensitive to human disturbance or have ecological requirements that do match these new environments.

### Box 3: Spatio-temporal overlap with humans in anthropogenic environments

Humans and their activities can impact spatio-temporal behaviors of a species. In anthropogenic landscapes, species can have a spatial and temporal overlap with humans or, on the contrary, have a spatial and temporal avoidance. Some species can have a spatial overlap but temporarily avoid humans, enabling them to use human-modified habitats, whereas others will spatially avoid humans but be active at the same time. Species using human-dominated habitats can adjust their behavior at a fine scale to avoid human encounters.



**FIGURE 3:** Spatio-temporal overlap between humans and mammals in an anthropogenic context, reproduced and adapted from Van Scoyoz et al. (2023)

## 4 | Aim and objectives of this *PhD* thesis

As it is not possible to preserve worldwide biodiversity in size-limited protected areas, the ecology of reconciliation is prone to explore ways for human and wildlife to cohabit by maintaining favorable spaces for wildlife in anthropogenic areas (Rosenzweig 2003). The key to sharing space between humans and wildlife is coexistence, defined as a “*dynamic but sustainable state in which humans and wildlife co-adapt to living in shared areas where human interactions with wildlife are governed by effective institutions that ensure long-term wildlife population persistence, social legitimacy, and tolerable levels of risk*” (Carter & Linnell 2016). The conditions for coexistence in human-modified environments will therefore depend on the degree of spatio-temporal overlap of a species with humans and the degree of anthropogenic resources consumed by a species, that humans can tolerate. Mutual adaptation of wildlife and humans, leading to coexistence, is inevitable for conserving biodiversity (Carter & Linnell 2023). Understanding the role of urbanized and agricultural matrices in conservation is essential to prevent the erosion of mammals in human-modified landscapes (Ferreira et al. 2018). It requires to understand if human structural habitats could be functional for other organisms and measure if our anthropogenic habitat can be suitable for wildlife (Dyck 2012).

The aim of this *PhD* thesis was to document the spatio-temporal use of multifunctional anthropogenic landscapes by African mammals, in order to find how to conciliate multiple human activities with African mammal conservation. More knowledge on the spatio-temporal niche of mammals in human-dominated areas is needed to be able to design adequate measures for coexistence. Studying the biology of anthropodependent, anthropophilic, synanthropic and anthropophobic species could then be crucial to predict the abilities for wild species to live in human-dominated habitats (Hulme-Beaman et al. 2016). My study took place in the multifunctional landscape of the Garden Route Biosphere Reserve (GRBR), in South Africa. The Garden Route National Park (GRNP) has the specificity to be a non-fenced protected area surrounded by human activities, making it the ideal location to study the coexistence between African mammals and humans. Multifunctional landscapes can be challenging for monitoring African mammals as they regroup a diversity of land-uses and multiple stakeholders. Therefore, we used two different methods of monitoring. First, I set-up camera traps (CTs), a classical method to monitor mammals. I began by experimentally validating the optimal height of CTs to test human and wildlife interactions in order to have the most accurate detections (chapter 1, manuscript 1). Then, I studied the spatial use of anthropogenic landscapes by mammals, along different land-uses and gradients of human disturbances (chapter 1, manuscript 2). As temporal human avoidance is a classical response of mammals (Gaynor et al. 2018), I also studied the temporal overlap between mammals and

human activities in areas with different levels of human disturbances, (chapter 1, manuscript 2). Anthropogenic landscapes are often areas of high human density, I used an increasingly common approach to wildlife monitoring: local ecological knowledge, *i.e.* the knowledge of the people living with their natural environments (Brook & McLachlan 2008; Bonney et al. 2009). I investigated the possibility of using LEK to explore mammal occurrence and its drivers, while informing on fine scale habitat use and human practices (chapter 2, manuscript 3). In order to obtain a global understanding of mammal ecology in anthropogenic landscapes, I tested the comparability of CTs and LEK to detect mammals in anthropogenic landscapes (chapter 3, manuscript 4). Finally, I used the previous results to combine CTs and LEK data, while increasing the spatial coverage of our study, to identify the life history traits enabling African mammals to persist in anthropogenic landscapes (chapter 3, manuscript 5). We used complementary methods to describe and understand mammal occurrence in anthropogenic landscape, always keeping the anthropodependence framework in mind (Hulme-Beaman et al. 2016). The results of this *PhD* thesis will hopefully help researchers to predict species and communities that are able to remain in those areas and implement adequate conservation measure to avoid a homogenization of mammal communities (Newbold et al. 2018; Suraci et al. 2021).



# General materials and methods

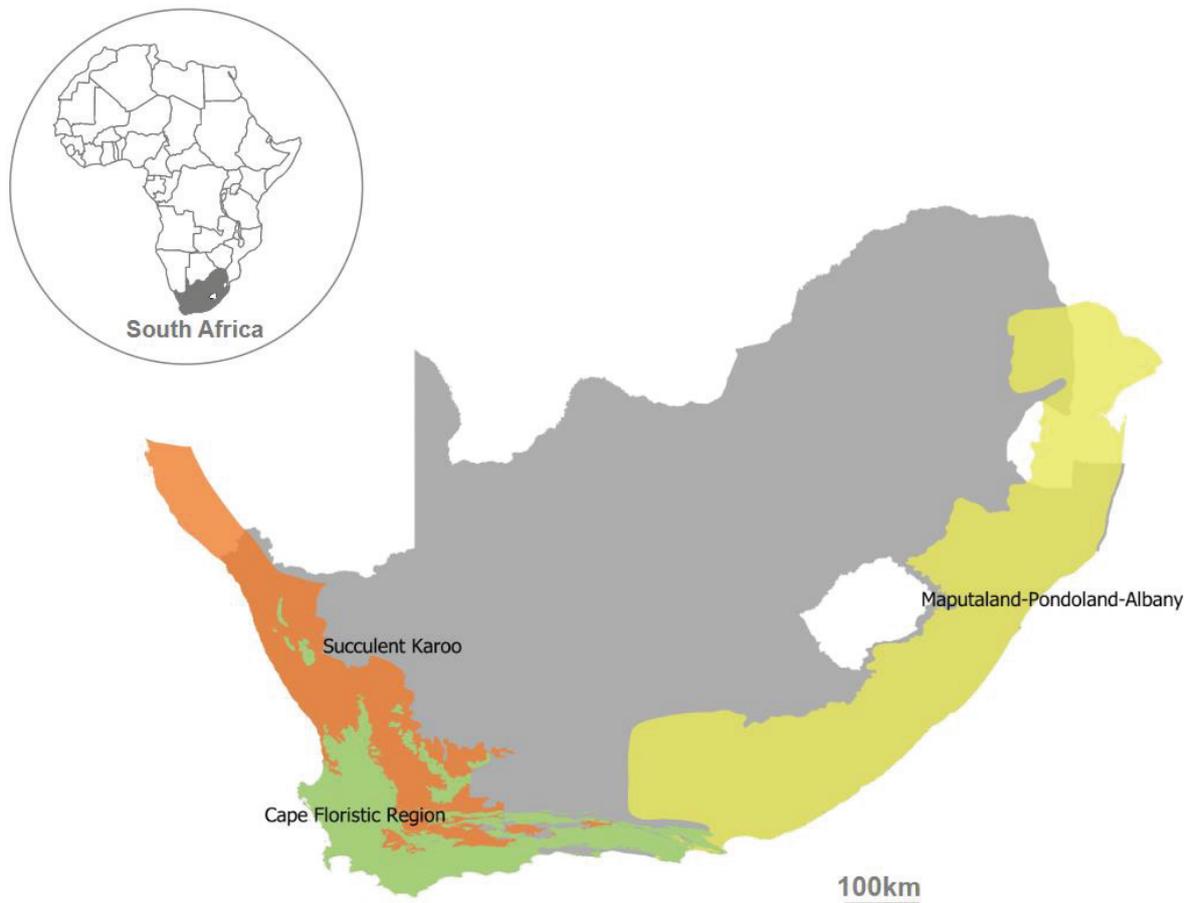




## 1 | Study area

### 1.1 | The Cape Floristic Region, hotspot of biodiversity

Biodiversity hotspots are defined by their high concentration of endemic species, facing significant habitat loss. They are a tool to designate conservation priorities (Marchese 2015). In 2000, the global list of hotspots included 25 areas, which contained 44% of all vascular plants and 35% of all vertebrate species, on only 1.4% of the terrestrial land (Myers et al. 2000). There are presently 36 recognized hotspots of biodiversity (Weinzettel et al. 2018). With 562 vertebrate species, 53 of which are endemic, the Cape Floristic Region has been identified as a hotspot of biodiversity (Figure 4) (Weinzettel et al. 2018). The remaining primary vegetation of the area represents only 24.3% of its original extent (Myers et al. 2000). The area is particularly threatened by agricultural expansion for domestic consumption (Weinzettel et al. 2018).



**FIGURE 4:** Map of the hotspots of biodiversity in South Africa (grey), Africa (top left), downloaded from Hoffman et al. (2016a).

## 1.2 | The Garden Route District Municipality

### 1.2.1 | Historical aspects

The Cape region was originally occupied by Khoikhoi and San people, who were hunters-gatherers. The Cape settlement was founded in 1652 by the Dutch East India Company (Fauvelle 2006). The town of George was founded in 1811. It was a woodcutter post since 1776, because it was in a strategic position for the timber industry (Baard et al. 2015). The exploitation of the indigenous forest started around 1763 and kept running for 200 years (Baard et al. 2015). As the demand for wood grew, the government began to exploit Tsitsikamma forests in 1830s (Baard et al. 2015). The exploitation seriously impacted forest integrity, and in 1847, a few patches of forests were closed from harvesting for recovery (Baard et al. 2015). They reopened only few years later, in 1856, because of the high demand for timber (Baard et al. 2015). The Forestry Department was created in 1880, and efforts towards conservation started to flourish (Baard et al. 2015). The first real protection for the forest was established in 1888 with the Cape Forest Act, exotic timber plantations were established to stop the harvesting of the indigenous forest (Baard et al. 2015). However, the indigenous forest was only closed for exploitation in 1940 (Baard et al. 2015). A forestry research station was founded in 1964, in George, which is now the George campus of Nelson Mandela University (Baard et al. 2015). The Garden Route National Park (GRNP) was established in 2009 to protect the indigenous forest and is not fenced (Baard et al. 2015). The GRNP was historically home to species now extinct from the area such as: lion (*Panthera leo*), black rhinoceros (*Diceros bicornis*), hippopotamus (*Hippopotamus amphibious*), buffalo (*Syncerus caffer*) and Cape mountain zebra (*Equus zebra zebra*) (Baard et al. 2015). Some species can still be found in private game reserve in the GRDM and the GRNP is now home to the last solitary elephant cow (*Loxodonta africana*) (Moolman et al. 2019).

### 1.2.2 | Ecological situation

The study area is located in the Garden Route District Municipality (GRDM), one of the five districts of the Western Cape in South Africa. The area includes a variety of biomes such as Afrotropical forests, diverse types of fynbos as well as wetlands, lakes, riverine and coastal habitats (Figure 5) (Baard et al. 2015; SANParks 2020). The GRDM host the diverse fynbos biome, endemic to South Africa, as well as Southern Cape Afrotropical Forest, forming the largest indigenous forest in Southern Africa (Figure 5) (Rebelo et al. 2006; Baard et al. 2015). Between 2017 and 2018, the GRDM suffered major fires that burned over 90,000 ha, forcing residents to be evacuated and, having largely unknown consequences for wildlife (Jenner 2018). Invasive plant species are a real threat to the vulnerable habitats found in the GRDM (Baard & Kraaij 2019). Summer is considered to be from November to March, whereas winter

is around June to August (Baard et al. 2015).. The annual rainfall in the area is between 600-700 mm. Months between September to March are usually rainier (Baard et al. 2015). The temperatures range from 15 to 25°C in summer and 7 to 19°C in winter (Baard et al. 2015).

### 1.2.3 | Economical situation

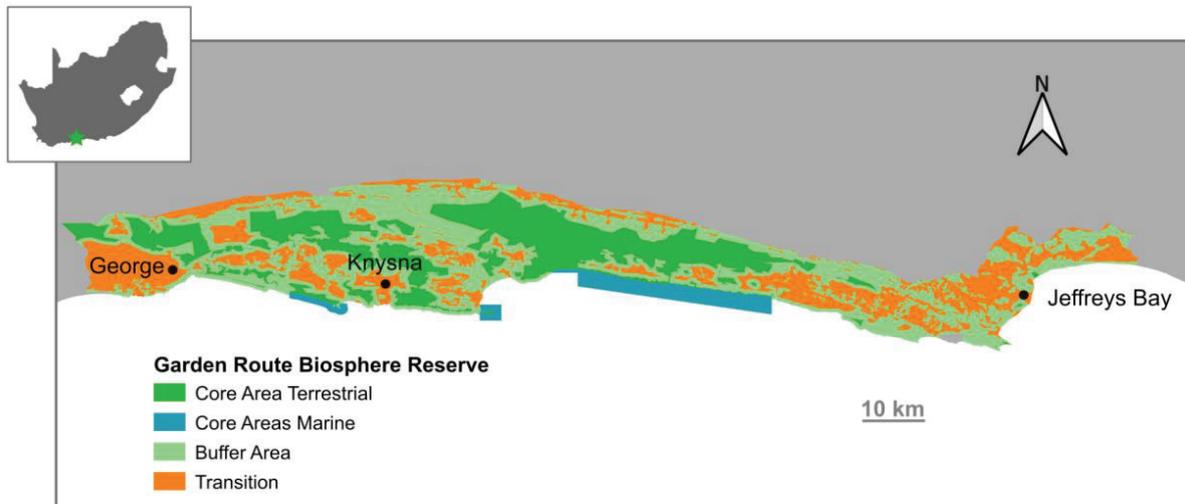
Since 1930, the number of suburbs and residences within the study area has increased drastically, with a peak in the 1960s, when nine suburban districts appeared (Crisp 2015). The population is expected to keep growing (Western Cape Government 2019). The population density of the GRDM was around 27 people/km<sup>2</sup> in 2019 (42 people/km<sup>2</sup> in George District, 69 people/km<sup>2</sup> in Knysna District) (Western Cape Government 2019). Human transformation was associated with multiple land-uses such as exotic tree plantations, crops and dairy farming, and urban and peri-urban developments intercepted by a vast road network (SANParks 2020). Chickens, sheep and cattle are the main livestock of the GRDM, representing 31%, 31% and 18% of the animals bred (Pienaar 2020). Lucerne, pastures and wheat are the major crops planted in 2017 in the GRDM (Pienaar 2020). The production of nuts and avocados (*Persea americana*) increased in the past years, mostly for exportation (Pienaar 2020).



**FIGURE 5:** Landscape Diversity of the Garden Route District Municipality: a) typical landscape mosaic, b) pine plantation, c) crops farming, d) peri-urban area, e) view of the Knysna river and the Gouna section of the GRNP, f) wetlands, g) thicket, h) Afrotemperate forest, i) river in Afrotemperate forest, j) fynbos, k) coastline and l) pasture.

### 1.3 | The Garden Route Biosphere Reserve

The Garden Route Biosphere Reserve (GRBR) was recognized by UNESCO as South Africa's 9<sup>th</sup> Biosphere Reserve (Pool-Stanvliet & Coetzer 2020). The GRBR goes from the town of George in the West to St Francis and Jeffreys' Bay in the East, and is located between the Indian Ocean and the Outeniqua mountains. Approximately 500,000 inhabitants live in the GRBR. The objective of the GRBR is to find local solutions for global problems, by developing interdisciplinary research to understand social ecological systems (UNESCO 2019a). Biosphere Reserves are part of the UNESCO's Man and the Biosphere Program and are the ground for research involving the local stakeholders (UNESCO 2019b). Biosphere Reserves include a strictly protected core, a buffer and a transition area (UNESCO 2019b). The GRNP is the core area and represents 31% of the GRBR (Figure 6). The GRNP contains remote zones and areas where visitors can practice various activities such as hiking or canyoning (Roux et al. 2020). The buffer zone, directly surrounding the core areas, includes scientific, training and education activities which must be in line with ecological practices. The buffer zone represents 41% of the GRBR. Transition area is the place for sustainable economic and human activities, which have to respect social and ecological values (UNESCO 2019a). This area represent 28% of the GRBR (UNESCO 2019a).

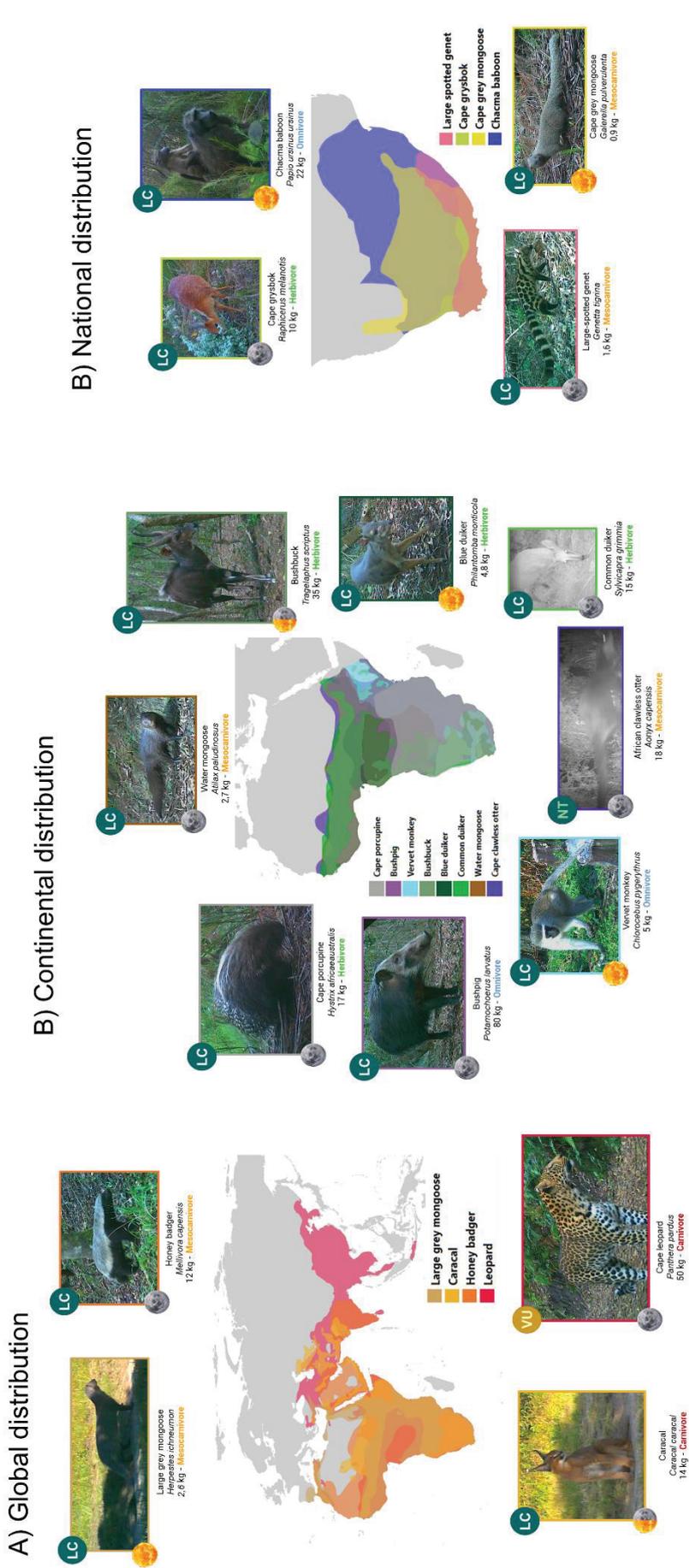


**FIGURE 6:** Map of the different sections of the Garden Route Biosphere Reserve (CapeNature 2016). The green star indicates the localization of the Garden Route Biosphere Reserve in South Africa.

## 2 | Study species

Only few studies have focused on the mammal species of the GRBR, and the conservation status of their populations is largely unknown, which makes this area of high interest for research (Baard et al. 2015). The list of potential mammals occurring in the GRNP contains 25 species above 500 g, but recent proof of presence is unavailable for some of them (Baard et al. 2015).

In this *PhD* study, I focused on 16 mammal species, which were confirmed to occur in the study area by a camera traps (CTs) survey (Figure 7). Most of them are considered 'least concerned' on the IUCN list, except for the Cape leopard (*Panthera pardus*), considered 'vulnerable', and the Cape clawless otter (*Aonyx capensis*), considered 'near threatened' (IUCN 2022). The leopard, caracal (*Caracal caracal*), honey badger (*Melivora capensis*) and large grey mongoose (*Herpestes ichneumon*) have wide distribution across Africa into South Asia (Figure 7). Other mammals from the GRBR are mainly occurring on the African continent (bushbuck *Tragelaphus scriptus*, blue duiker *Philantomba monticola*, common duiker *Sylvicapra grimmia*, African clawless otter, vervet monkey *Chlorocebus pygerythrus*, bushpig *Potamochoerus larvatus*, porcupine *Hystrix africaeaustralis* and water mongoose *Atilax paludinosus*) (Figure 7). Four species have a national distribution range, making their conservation in the GRBR very important: the Cape grysbok *Phicinus melanotis*, chacma baboon *Papio ursinus*, large-spotted genet *Genetta tigrina* and Cape grey mongoose *Galerella pulverulenta* (Figure 7). Mammals of the GRBR have diverse characteristics, which makes it very interesting for the comparison of their ability to persist in human-dominated landscapes (Table 1). The species have different position in the trophic community: carnivores, mesocarnivores, omnivores and herbivores, with a gradient of diet diversity (Figure 7, Table 1), and diverse home-range size, testifying of their ecological requirement (Table 1). Some live in large or family groups, while most are solitary (Table 1). The species showcase a gradient of litter size, length of gestation, age at sexual maturity and longevity (Table 1). All these traits may induce various responses to environmental and anthropogenic land-uses, which is why this community is adapted to our study. This *PhD* thesis focused on mammal species over 500g because (1) they are big enough to be monitored with camera traps, (2) they are more easily identified by people than other groups such as birds or insects.



**FIGURE 7:** Distribution range of the diverse mammal species occurring in the Garden Route Biosphere Reserve, South Africa, downloaded from the IUCN Redlist (IUCN 2022). The common and scientific name is specified for each species, as well as their body mass and diet. The conservation status is indicated on the top left of each photograph. The sun at the bottom left indicates that the species is diurnal, the moon, nocturnal and crepuscular species are identified by half a sun and half a moon. Photographs were taken during the camera traps survey, excepted for the common duiker, which photograph was sent by Scott Thomson from the Great Brak River Conservancy.

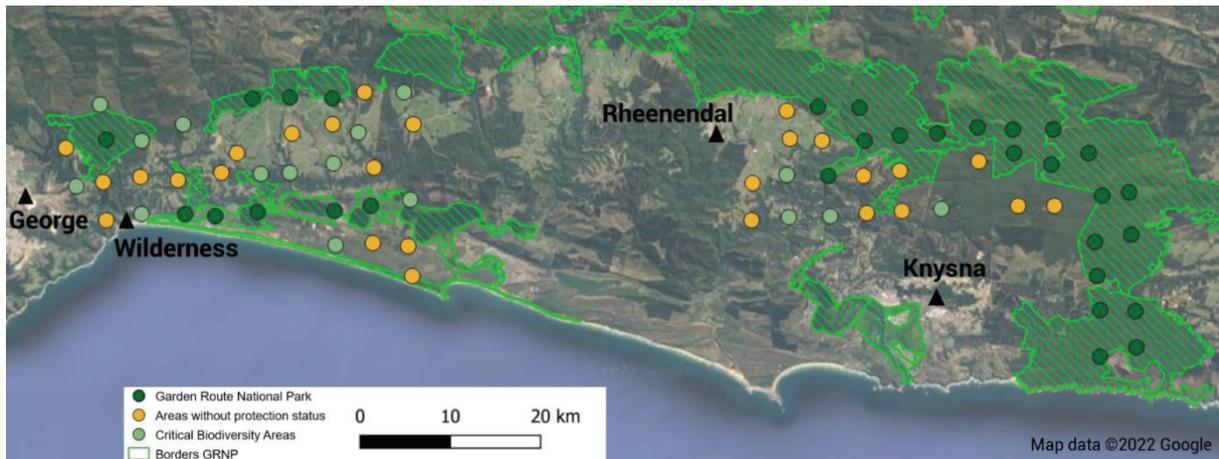
**TABLE 1:** Description of the traits of each species extracted from EltonTraits and PanTHERIA database (Jones et al. 2009; Wilman et al. 2014).

<b>Common name</b>	<b>Order</b>	<b>Diversity of diet</b>	<b>Body mass (g)</b>	<b>Gestation length (d)</b>	<b>Home range (km<sup>2</sup>)</b>	<b>Average litter size</b>	<b>Longevity (m)</b>	<b>Solitary or social</b>	<b>Sexual Maturity age (d)</b>
<b>African clawless otter</b>	Carnivora	0.50	18999.84	62.99	99.74	2.62	132	Social	371.23
<b>Blue duiker</b>	Artiodactyla	0.80	4896.05	205	0.006	0.98	144	Solitary	351.59
<b>Bushbuck</b>	Artiodactyla	0	43250.39	182.5	0.02	1	156	Solitary	431.61
<b>Bushpig</b>	Artiodactyla	1.19	48781.25	121.73	4.47	2.73	240	Family	585
<b>Cape grey mongoose</b>	Carnivora	0.80	797	50	3.81	2.25	104.5	Solitary	591.83
<b>Cape grysbok</b>	Artiodactyla	0.33	10249.91	210	0.38	1	168	Solitary	630
<b>Cape porcupine</b>	Rodentia	0.5	14936.02	93.49	1.31	1.51	240	Family	438.45
<b>Caracal</b>	Carnivora	0	13749.91	71.47	293.94	2.3	204	Solitary	437.27
<b>Chacma baboon</b>	Primates	1.47	17729.44	185.92	9.12	1.01	540	Social	1543.35
<b>Common duiker</b>	Artiodactyla	0.80	15639.15	174.89	1	0.98	171.96	Solitary	293.14
<b>Honey badger</b>	Carnivora	1.47	8500	181.46	350	2.35	318	Solitary	270
<b>Large grey mongoose</b>	Carnivora	1.50	2980.02	75.87	2.18	3	240	Solitary	729.99
<b>Leopard</b>	Carnivora	0	52038.22	96.74	123	2.14	276	Solitary	810.68
<b>South African large-spotted genet</b>	Carnivora	0.80	2066.57	71.48	0.04	2.76	180	Solitary	841.82
<b>Vervet monkey</b>	Primates	1.33	4993	140	1.72	1	384	Social	1825
<b>Water mongoose</b>	Carnivora	1.28	3299.97	77.27	1.73	2	209	Solitary	234.83

## 3 | Main methods

### 3.1 | Camera trap survey

Camera trap (CT) surveys are a non-invasive method of monitoring wildlife over a long period of time (O'Connell et al. 2011; Cordier et al. 2022). The Snapshot Safari Project has the objective of monitoring and understanding the diversity of mammal species across South Africa (Pardo et al. 2021). They are using a standardize method to be able to compare the 39 sites present in Africa, including 30 sites in South Africa (Pardo et al. 2021). To choose the location of the CTs, a grid of 5 km<sup>2</sup> is placed on a map of the future study site. CTs need to be set-up as close as possible to the center of each grid cells (Pardo et al. 2021). Because of the particular context of the GRBR, mixing protected areas, private properties, farms and pine plantations, I had to be in contact with many people to set-up the CTs grid. In the GRNP itself, I was helped by Melanie de Morney and Lizette Moolman, from South African National Parks (SANParks). Their experience and knowledge of the park made it easier to set-up the cameras. Outside the GRNP, the task was longer and more tedious as I had to identify and contact the landowner of each site where the CT point was. After many encounters, I completed my list of land owners and meet them. In total, I contacted 31 stakeholders (17 farmers, 10 residents, 2 foresters). I presented the aim of the study to each of them and they all agreed to be involved in the project. It took me one month and a half to set-up 75 CTs in the GRBR, 30 CTs were set-up in the GRNP, the rest were set-up outside (Figure 8). A more detailed protocol can be found in the chapter 1 (manuscript 2). I checked cameras every two to three months with the help of a SANParks agent or a Nelson Mandela University student to change the batteries and SD cards. The survey was conducted from the 2<sup>th</sup> of February 2021 to the 20<sup>th</sup> of May 2022 (15 months), resulted in 29,392 trap nights. I did the service of the CTs five times, and each field session lasted about twelve days. One CT was stolen before the first service. Another CT was stolen four months after being installed in a private property, but the landowner found it few days later and the CTs were reinstalled three weeks later. Three more CTs were stolen in May 2022 after 15 months of survey.



**FIGURE 8:** Site of the camera traps study in the Garden Route Biosphere Reserve, South Africa. The dots represent the localizations of each camera trap, and are colored per type of protection: protected area in dark green, Conservation Biodiversity Area in light green and areas without protection status in yellow. The Garden Route National Park is represented in green stripes. The black triangles represent some of the towns of the area.

I manually tagged all the photographs, firstly by using digiKam (digiKam Team 2001), then with the online software TrapTagger (Osner 2022). Trap Tagger uses an artificial intelligence to assist the worker and reduce their error rate. It removes all empty photographs and only proposes photographs with something to identify. All mammal species and images with birds, rodents, humans, cyclists, motorcycles, vehicles, livestock, cats, dogs, poultry or horses were tagged.

After each camera services, I sent the best photographs to the landowner to make them aware of what was happening on their properties and trigger their interest. I did two presentations to SANParks rangers on preliminary results and I sent a summary of the descriptive results of the project to all the people involved. I received very positive feedbacks from everyone. The PowerPoint can be viewed at this link: [https://drive.google.com/file/d/1BxBpLvQRRXQKXvrVnRqBF7TsWUJb4hwh/view?usp=share\\_link](https://drive.google.com/file/d/1BxBpLvQRRXQKXvrVnRqBF7TsWUJb4hwh/view?usp=share_link).

### 3.2 | Citizen survey

To use local ecological knowledge, I developed a questionnaire to assess the presence of wild mammal species on human properties with the expertise of Chloé Guerbois. Due to covid-19 restrictions and to avoid face-to-face interviews, we decided to use the online website SurveyMonkey. The survey targeted all the landowners of the GRBR from Mossel Bay, George, Knysna and Bitou Municipalities. The draft questionnaire was tested with 20 residents between March and October 2021, to improve the understanding and make sure the questions

were adapted to the area. I asked key stakeholders such as person in charge of a conservancy or residents. Some landowners involved in the CTs survey also agreed to pilot the questionnaire. After each response I worked on the questions again to improve them. The final questionnaire included 59 questions, divided into nine parts (Table 2). One section was on the characteristics of the property, one section on the mammal occurrence on the property and in the neighborhood, one section on the mammal activities on the property, one section on the human activities occurring on and the domestic animals present, one on the impact of human infrastructures on mammals and a last part on their relation to wild mammal species. We added a few knowledge questions to assess the reliability of the data collected. The questionnaire can be found in **Appendix 1**. When the survey was ready, I sent it using: conservancies mailing list obtained thanks to CapeNature, SANParks mailing list of landowners of the GRBR, WESSA mailing list, multiples WhatsApp groups on wildlife as well as Facebook groups of the different municipalities. We also published the link to the survey in local newspapers (George Heralds, The Edge). We send several reminders to launch as many people as possible. We did not get many responses from residents in Mossel Bay, which emphasizes the importance of finding the adequate people to relay online surveys. The questionnaire was designed in English and was translated into Afrikaans. Participation was voluntary and anonymous. The survey link was accessible online from November 2021 to March 2022. Once the survey was closed, I sent descriptive results to everyone who asked for feedback. The PowerPoint can be viewed at this link:

[https://drive.google.com/file/d/1UiKROc7xch0Q699jIWC\\_5cGx08szDCY/view?usp=share\\_link](https://drive.google.com/file/d/1UiKROc7xch0Q699jIWC_5cGx08szDCY/view?usp=share_link). A more detailed protocol can be found in chapters 2 and 3 (manuscripts 3, 4 and 5). This research was approved by Nelson Mandela University human ethic committee (H20-SCI-SRU-002).

**TABLE 2:** Summary of the different parts of the online survey.

Topic	Parts	Number of questions
<b>Mammals</b>	Mammals occurrence	6
	Mammals activities	3
	Mammals occurrence in the neighborhood	1
<b>Properties</b>	Description of the properties	7
	Human activities	8
	Interaction between domestic animals and mammals	8
	Impact of human infrastructures on mammals	7
<b>Perception</b>	Relation to mammals species and the Garden Route	15
<b>Knowledge</b>	Knowledge questions	4

### 3.3 | Unsuccessful protocols

The protocols described above are the ones that worked well, but things do not always go according to plan. I tried to collect other types of data during my *PhD*, but was unsuccessful and these will therefore not be mentioned in the following manuscripts. As I have put time and effort into these, I thought it was worthwhile mentioning in this section.

#### 3.3.1 | Assessing mammal anthropogenic resources consumption

In particular, we wanted to carry out macroscopic diet analyses to understand what species were consuming in human-modified habitats than those in protected areas, which could not be done in the time available. The plan was that when I started to set-up the CTs in March 2020, I would look for fresh scats, collect them and place them in a paper bag. However, I quickly realized that finding scats was more difficult than expected, because of the density of the vegetation and the large area to cover. In addition, because of the delay caused by the Covid-19 pandemic, I focused my time on deploying the CTs first, which prevented me from spending more time on collecting and analyzing the scats samples.

In February 2022, Elizabeth Kennedy-Overton did a six-month internship for her master 2 at IRL REHABS. I helped her to collect chacma baboon scats, in the same area the CTs were set-up, to assess the influence of the land use on baboons' diet. She followed troops of baboons in different land-uses: a troop in Nelson Mandela campus corresponding to peri-urban areas, a troop in Hoekwil corresponding to an agricultural area and two troops in Knysna to compare with individual mostly using natural forest habitats. She compared the isotopic ratios of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  along a gradient of landscape modification (paper in preparation).

### 3.3.2 | Assessing individual strategies in anthropogenic landscapes

I was supposed to study the movements of two mesocarnivore species, to examine possible individual strategies, by collaring them with a Global Positioning System (GPS) electronic tag. The aim was to study their movement in the anthropogenic matrices to highlight their spatial use and calculate their home ranges, and to compare these with their counterparts mostly using protected areas. The plan was to focus on two species of different body sizes: the caracal and the large-spotted genet. To follow their movements for a year, we planned on using LoRa/GPS collars from Africa Wildlife Tracking (AWT), attached with an adjustable collar, and with a cotton drop-off, that breaks after a certain amount of time. I started to carry out the protocol to capture large-spotted genets. In September 2021, on the George campus of Nelson Mandela University, I set up thirteen tomahawk traps. Traps were baited with chicken and sardines. Each trap was oriented and covered with brushes to provide some protection from exposure. Traps were set up in the late afternoon, at dusk, checked early the following morning at dawn, and left closed throughout the day. A dedicated veterinarian, Muller Strydom (BVSc), was part of the project to facilitate the darting and collaring. Three different large spotted genets were captured. We tried to fit the collars but they were too heavy and large for them. The collars were sent back to AWT so that they could reduce the weight and size of the collars. We set the 13 traps again in October 2021. After three days of trapping, we caught another genet. Unfortunately, the collars were still too wide for this species. Furthermore, we realized that the shape of the collars may have strongly affected their behavior, as they are a cavity and tree species (Widdows et al. 2016). We decided to go for a bigger species, which has been previously successfully collared by other teams: the caracal (Ramesh et al. 2017; Leighton et al. 2022b). In May 2022, we set-up six tophok Rooikat cages, in the same area for two months. We tried different baits, such as chicken, sardines, sent lures and tin foil balls. Unfortunately, although we had some sightings, the caracals were very difficult to catch and we failed. Finally, because of time restrictions, I stopped the experiment. It taught me lessons on the uncertainty of working with wild mammals.

My project was approved by SANParks (BERN-A/2020-008) and CapeNature (CN44-87-16198). The methods used were only non-invasive approaches, which can be interesting to use to monitor wildlife populations as they respect the 3Rs rule: Reduce, Replace, Refine (Russell & Burch 1959).



# Chapter 1

## Using camera traps to monitor African mammals in anthropogenic multifunctional landscapes



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Before studying the responses of mammals in anthropogenic landscapes using CTs data, it is important to confirm that the set-up used is relevant to reduce bias and obtain accurate data. In this chapter, we first confirmed in the manuscript 1 the adequate height for setting our CTs grid in order to detect mammals but also humans. Second, using the recommended height, we studied the spatio-temporal responses of mammals to anthropogenic variables of the landscapes (manuscript 2). Our results showed the diversity of strategies developed by mammals with species dependent on natural habitats (e.g. the blue duiker) and others more tolerant to human disturbance (e.g. the caracal), suggesting different cost-benefits, as envisaged by the anthropodependence hypotheses. Most species reduced the temporal overlap of their activity with humans in areas with high road density, while changes associated with distance to infrastructure were minimal. Combining information on habitat use and temporal responses to human disturbance has proven useful in understanding species responses to anthropogenic features. The manuscript 2 has not been peer-reviewed yet; it merits further work and the English needs to be corrected before submission.

Manuscripts associated to chapter 1:

- Manuscript 1: **Alice Bernard**, Lizette Moolman, Melanie A. de Morney, Chloé Guerbois, Jan A. Venter, Hervé Fritz. Height related detection biases in camera trap surveys: insights for combining data sets. Koedoe - African Protected Area Conservation and Science. April 2023. <https://doi.org/10.4102/koedoe.v65i1.1734>
- Manuscript 2: **Alice Bernard**, Lain E. Pardo, Lizette Moolman, Melanie A. de Morney, Chloé Guerbois, Jan A. Venter, Hervé Fritz. Spatio-temporal overlap between African mammals and humans in a multifunctional landscape: insights on the concept of anthropodependence

## Manuscript 1

### Height related detection biases in camera trap surveys: insights for combining data sets

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**Key words:** Camera trapping, detection zone, detection probability, mammal monitoring, wildlife survey methodology, conservation planning

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## 1 | Introduction

Camera trap surveys are a non-invasive method for monitoring wildlife (O'Connell et al., 2011). Camera traps inevitably record non-target species (Burton et al., 2015) and this by-catch is potentially useful (Edwards et al., 2011; Hofmeester et al., 2020; Mazzamuto et al., 2019). The usefulness of by-catch data is determined by the probability of capturing an animal within a given survey design (Findlay et al., 2020). As described by Findlay et al. (2020), an animal has to pass in front of (encounter probability), trigger (trigger probability) and be photographed by the camera (registration probability). The quality of the image must also be of sufficient quality to be able to identify the animal (capture quality probability). The probability of an animal triggering a camera trap differs between species and can be influenced by their body mass, size or behaviour, environmental variables (land cover, temperature), as well as camera trap brand, model and height of set-up (Apps and McNutt, 2018; Hofmeester et al., 2019; Kolowski et al., 2021; P. Meek et al., 2016; Swann et al., 2004). To ensure the highest registration and capture probabilities for a target species or to maximise the diversity of photographed species, camera placement is crucial (Burton et al. 20015). Camera height is one of the critical settings, though few studies have focused on it, whereas it has been shown to affect species detection (Anile and Devillard, 2016; Burton et al., 2015; Hofmeester et al., 2019; P. Meek et al., 2016; Palencia et al., 2021). Camera height settings usually differ between surveys aimed at monitoring human activities and surveys aimed at monitoring biodiversity (Burton et al., 2015). Little emphasis has been put on using by-catch data from surveys targeting humans for biodiversity monitoring purposes. We tested the effect of camera height on detection probability of mammal species by comparing a standard height for monitoring biodiversity (50 cm, used in the African Snapshot safari survey, Meek et al., 2016; Pardo et al., 2021) with a height chosen to monitor human related events (130 cm, used in a Human-Wildlife Interface monitoring project, Moolman et al., 2019). We hypothesized that lower cameras would detect smaller mammals at higher frequencies than the higher cameras, but that be no difference would occur between camera heights in detecting larger species. We aimed to assess if datasets from various surveys (humans or mammals as primary survey targets) using different camera heights could be combined. We also aimed to test whether one of the height settings could maximise the detectability of both human and other mammal species activity, in order to optimise camera trap survey design.

## 2 | Material and methods

### 2.1 | Study site

Ten passive infrared-triggered (Bushnell Trophy Cam HD Aggressor No Glow) cameras were set-up at five different locations in the Harkerville Section of the Garden Route National Park, in South Africa (-34.046731, 23.209715; Fig. S1). All cameras were deployed in Afrotropical forest, on hiking trails. Two cameras were set-up at each location, at two different heights, on the same tree, no further than one m away from the hiking trails (Fig. S1). High cameras were placed at a height of 130 cm ( $\pm 5$  cm) from the ground level of the trail, which was the set-up for the Human-Wildlife Interface survey, and low cameras at 50 cm ( $\pm 3$  cm), which is the average shoulder height of the mammal species (mean height= 57,1 $\pm$  31,9 cm; height range:

15 to 120 cm) in the area (Palencia et al., 2021). The two cameras were oriented and angled towards the same direction to photograph the same area. They were diagonally facing the trails, so that animals had to walk towards or away from the camera, to have a longer area of detection. We measured the horizontal and vertical shift from the high camera compared to the low camera: we identified 5 points on the low camera image and compared the relative position of these on the high camera by measuring the relative deviation on the photograph (Fig. S2A). The mean vertical deviation was 5% and horizontal deviation less than 2% between low and high cameras (Fig. S2B). The cameras used black flash (no glow), *i.e.* infra-red illumination, that prevents animals from being disturbed and being detected by humans at night. To reduce the risk of theft, cameras were protected by cable locks and metal casings. Cameras were active 24h per day and were set-up to take one 8 mega-pixels image per trigger, with a delay of one second between subsequent triggers. The sensitivity was set on 'normal'. The flash intensity was set on 'high'. Data were collected from 9 March 2020 to 6 August 2020. Humans moved cameras at two sites. Data from after they were moved were excluded from the analyses. Cameras were visited every three months to change batteries and SD cards. We ensured that the time set on the cameras was identical. When servicing the cameras, both cameras took pictures of the researchers walking towards them, hence the differences observed in the study were not induced by a malfunctioning camera.

## 2.2 | Data processing

The images were processed using the CameraBase software (Tobler, 2007). For each image, the species name and the number of individuals were manually tagged, while the software automatically extracted the time and date of each photograph. Humans, their activities (walking, motorcycling), vehicles and dogs were tagged as such (Table S1). When an image was dark, we adjusted the brightness. When it was not possible to identify a species because only a part of it was visible, the photograph was tagged as ***non-identified***.

In order to test the impact of camera height setting from these two types of surveys on the analysis of a potential combined dataset and because we had an average of 9.5 photographs for each event, we only kept photographs from the same camera and with the same species that had a minimum period of 30-minutes between image time stamps. This procedure is standard practice to obtain a list of independent capture events for camera trap data analysis, and we wanted to position our comparison within commonly used practices. We merged the similar events of both camera heights for a given location by date and time ('merge' function, 'base' package), in order to produce a comparative list of all the different capture events per camera. When the two cameras were triggered simultaneously and successfully captured the same event, we classified the pair as ***identical***. Events that could not be identified on either camera were deleted (Hofmeester et al., 2020). For the events that were not similar between the two cameras, we manually processed the remaining capture events by comparing the images of both cameras. When only one of the two cameras was triggered, meaning that we could not find any photograph for the other camera at that time, we classified this capture event as ***not triggered***. When the image of one of the two cameras was empty (*i.e.*, only background vegetation is visible but no mammal or human), we coded the photograph as ***empty*** and when a camera was triggered but it was not possible to identify any species, e.g. because the image was too dark even after adjusting the brightness, we classified it as ***dark***. For each non-identical event (*i.e.* events classified as not triggered, empty or dark), we specified the species

that was detected by the other camera. We noted the information in Excel. **Not triggered** capture events corresponded to a non-trigger, **empty** images to a lack of capture by the camera and **dark** images to a poor image quality (Findlay et al., 2020).

Finally, each capture event was categorised according to whether it was taken during the day or at night based on the sunset or sunrise time ('sunrise.set' function, 'StreamMetabolism' package).

### 2.2.3 | Data analyses

All statistical analyses were performed in R (R Core Team, 2020) and all the graphics were plotted using the 'ggplot2' package (Wickham, 2016).

#### 2.2.3.1 | *General detection model*

To compare the detection similarity of different species and human activities between the two treatments (low camera vs high camera) we assigned a 0 for events classified as not triggered, empty or dark or a 1 for identical events. We built a generalised linear model to perform a logistic regression, *i.e.* with a binomial distribution of the response variable, to explain the detection of the cameras. We used the "MASS" package (Venables and Ripley, 2002), and included the site as a variable to control for deviation between two cameras at the same site. We also tested the influence of the period of the day (day vs night) on the detection probability. For each detected species, the average weight and height were compiled to test how they could affect the variation in detection between camera heights (Child et al., 2016; Hofmeester et al., 2020) (Table S1). Weight and height were log-transformed to conform with parametric modelling constraints. Thereafter, we used a backward stepAIC model selection procedure ('stepAIC' function, 'MASS' package), to search for the best combination of variables to get a simplified model. The predicted detection probabilities were calculated ('predict' function, 'car' package) and plotted ('ggpredict' function, 'ggeffects' package) (Fox and Weisberg, 2019; Lüdecke, 2018).

#### 2.2.3.2 | *Species detection and by-catch frequency*

For each event, we independently performed a McNemar test ('mcnemar.test' function, 'stats' package), which compares the proportions of paired data to highlight species for which there were differences in the number of detections between the two camera heights. We also plotted the type of non-identical events (not triggered, empty, dark), coloured by species to describe the causes behind discrepancies between paired cameras.

## 3 | Results

The camera trap survey ran over a period of 150 days. Camera pairs were collectively active for a total of 595 trapping days and produced 15 623 photographs, corresponding to 987 capture events. Most of the photographs were taken during the day (70% for high cameras and 62% for low cameras). Low and high respectively accounted for 53% (519) and 47% (468) of the captures. These corresponded to 559 unique independent events recorded during the trapping survey. Low and high cameras respectively captured 90% and 81% of the events.

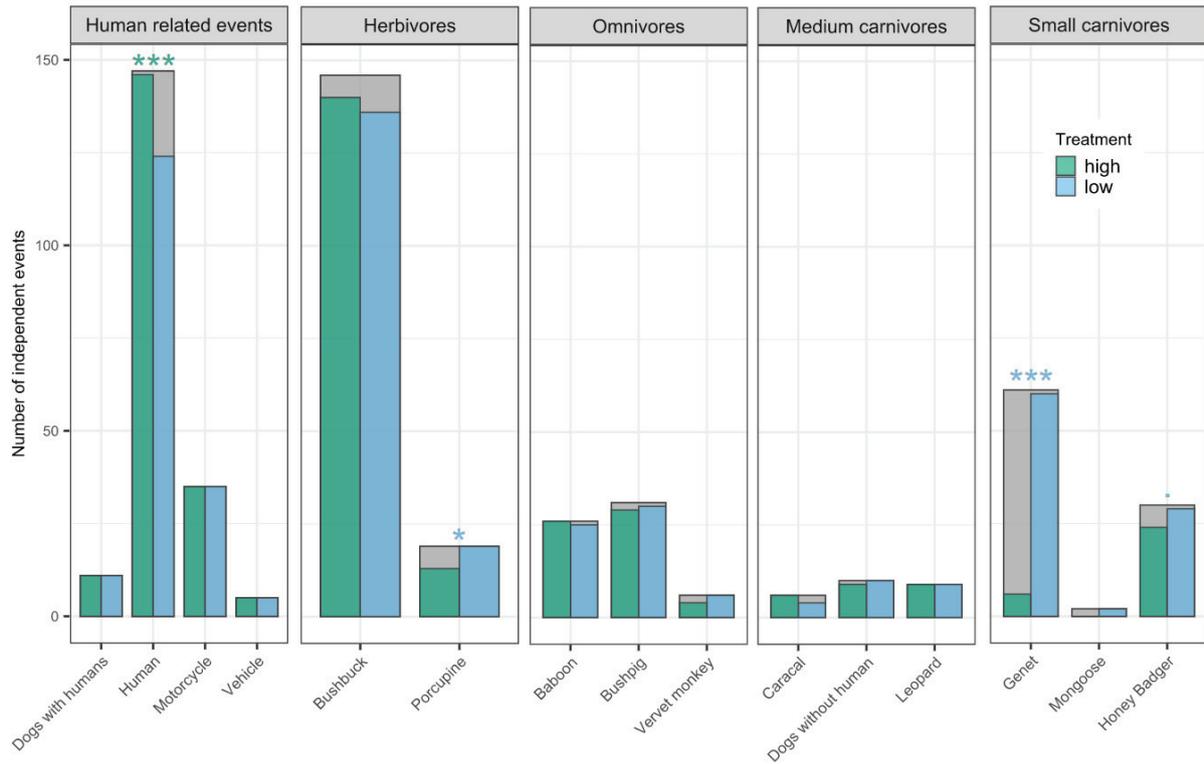
The high cameras missed 16% of the events (90) compared to 9% for the low cameras (48). The percentage of empty photographs was fairly low for both heights, but was twice as low for the low cameras (0.6% for low cameras and 1.8% for high cameras). The most frequently captured species were bushbuck (n=146) and humans (n=147). Cape grey mongoose (n=2), vervet monkey (n=6) and vehicles (n=5) were the rarest (Table S1). Ten wild mammal species were identified from the survey: chacma baboon (*Papio ursinus*), honey badger (*Mellivora capensis*), bushbuck (*Tragelaphus sylvaticus*), bushpig (*Potamochoerus larvatus*), caracal (*Caracal caracal*), South African large-spotted genet (*Genetta tigrina*), Cape leopard (*Panthera pardus*), vervet monkey (*Chlorocebus pygerythrus*) Cape grey mongoose (*Herpestes pulverulentus*) and Cape porcupine (*Hystrix africaeaustralis*).

### 3.1 | General detection model

High cameras detected more humans than low cameras (respectively 146 and 124), whereas high cameras detected less wild mammal species events than low cameras (266 and 330 respectively). The best model includes three significant interactions. Low cameras were more efficient in detecting smaller species (weight and height) than high cameras (p-value: 0.00539, Fig. S3; Table S2). Additionally, lower cameras were more efficient for detecting species at night (p-value = 0.00940, Table S2), especially smaller species (p-value: 0.00798, Fig. S3; Table S2). The site was not part of the selected variables, so we assumed that it had no effect on the difference in detection probability between the two camera heights (Table S2).

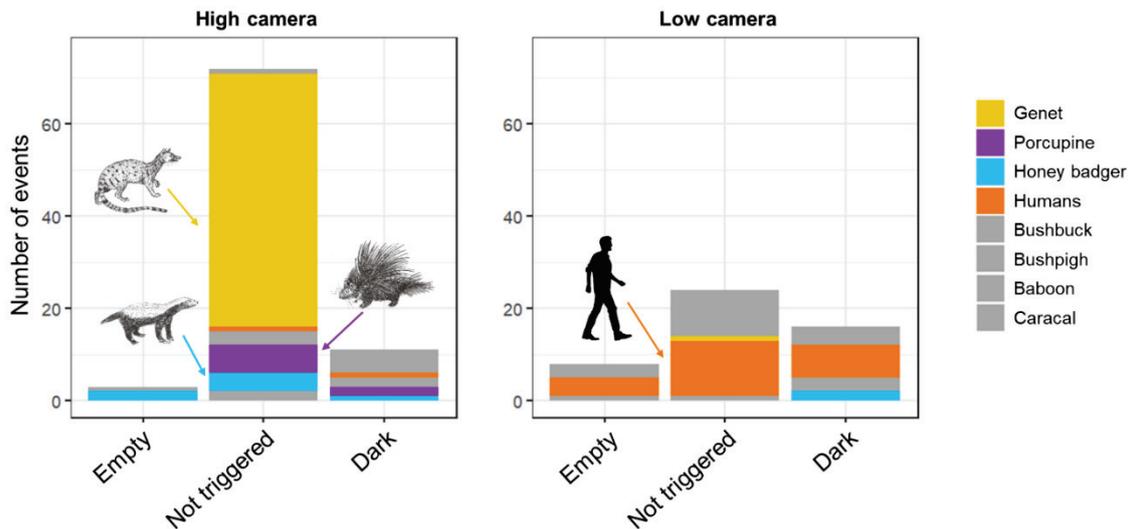
### 3.2 | Species detection and by-catch frequency

The only species not detected by high cameras, the Cape grey mongoose, was detected only twice by low cameras. We found that high cameras were less effective at capturing porcupine (p-value: 0,014), large-spotted genet (p-value: 5,35E-13), and honey badger (p-value: 0,059), compared to low cameras (Table S3, Fig. 1). Low cameras detected most of the human-related events (*i.e.*, vehicles, motorcycles and dogs with humans) but had a lower detection success for humans (p-value: 7,10E-06). Furthermore, for some species (bushbuck, human, bushpig, large-spotted genet and honey badger), the total sum of detections (in grey on Fig. 1) was greater than the maximum number of detections for each camera, proving that both cameras missed some images.



**Fig. 1:** Number of independent detections by low (blue) and high (green) cameras for each species photographed in the Harkerville forest, Garden Route National Park, Western Cape, South Africa. Grey represents the total number of independent detection event.  $P: 0.05 > * > 0.01 > ** > 0.001 > ***$

The non-identical events were mostly due to cameras not being triggered by a by-catch species, which concerned small mammal species for high cameras (e.g. 63% of genets not detected) and humans for low cameras (56% of the non-detected events; Fig. 2).



**Fig. 2:** Type and number of non-identical events for A) high camera and B) low camera, coloured by species and sorted by empty images, not triggered events, and technical issues.

## 4 | Discussion

Lower placed cameras were more effective for capturing small and nocturnal mammals while higher cameras did marginally better at detecting humans and large nocturnal species. This may be because humans are bipedal and have a higher centre of gravity than quadrupedal species, with the bulk of their mass being higher (Alexander, 2004; Soni et al., 2020). Moreover, the high cameras missed the detection of most large-spotted genets and all Cape grey mongooses, which were by-catch species. This might be because species walked under the triggering sensor of the camera or that the latter was too far to detect smaller species, which is consistent with other work showing that missed detections were the result of failed triggers that increased as species size decreased (Jacobs and Ausband, 2018). This supports that a setup height which is not adapted to the target species misses most of its detections, mainly because the cameras are not triggered, and not because of the registration or capture quality probability (Findlay et al., 2020). As the cameras from both heights were oriented to photograph the same vertical line area (Fig. S2), the non-identical events were mostly due to the blind spot from the high camera (near the ground at the bottom of the tree) or because the individual moved outside of the range of detection of the motion sensor. Empty photographs were most likely due to species triggering the camera and moving out of the detection zone too quickly to be photographed (Findlay et al., 2020).

Our survey focused on a single camera trap model, at five sites, all distributed in the same habitat and at the same distance of a trail, in order to test for the effect of camera height on detection. We did not take into consideration other survey designs that might impact the detection. Our results showed that cameras set-up higher from the ground are not suitable for studying small mammals (under 30 cm and 10kg), however, the by-catch data can be used for studying human activities and large mammals (above 50cm or 20kg). Furthermore, the low cameras appeared to be the most relevant for studying the biodiversity of small to medium-sized mammals (mean height =  $57,1 \pm 31,9$  cm, height range: 15 to 120 cm). Using cameras set at a low height is suitable for the study of human/wildlife coexistence, as by-catch of human related events was high. Our study expands knowledge on how to incorporate by-catch data into camera trap studies by providing a case study comparing human-focused surveys with mammal-focused surveys in forest habitat. Camera trap by-catch should not be carelessly used to address a multitude of research objectives, as camera height can limit such investigations. Pilot studies are paramount before merging datasets acquired from surveys with differing objectives and camera trap set-ups, in order to understand the limitations of such combined datasets and what it can be used for.

We concur with other studies that found a significant effect of the camera height on species detection (Findlay et al., 2020; McIntyre et al., 2020; Meek et al., 2016) and that the probability of detection for cameras positioned at different heights, depends on the species size-class (Palencia et al. 2021). It confirms the necessity to adapt the height and the angle of the camera according to the targeted species or community of species to optimize detection rate (Hofmeester et al., 2020; McIntyre et al., 2020; Meek et al., 2016). Our results were obtained in dense forest, which can limit the potential area of movement for the species and the detection range of the cameras, yet they are similar to results found in open landscapes (McIntyre et al, 2020; Palencia et al. 2021). We support many authors in concluding that by-catch data can play a crucial role in providing valuable information on management, conservation and environmental processes (Edwards et al., 2018; Hofmeester et al., 2020), if imperfect detection is accounted for when combining different studies of camera traps (Hofmeester et al., 2019). Failure to take into consideration the effect of camera height on animal detection will lead to poor quality data, and will likely bias analysis, interpretation and conservation outcomes.

## Acknowledgements

The authors thank South African National Parks for allowing this study in the Garden Route National Park, and the rangers who assisted with the service of the cameras. The authors thank Jérémy Tornos for his help at various stages of the work as well as Justin Bellengé for the drawings.

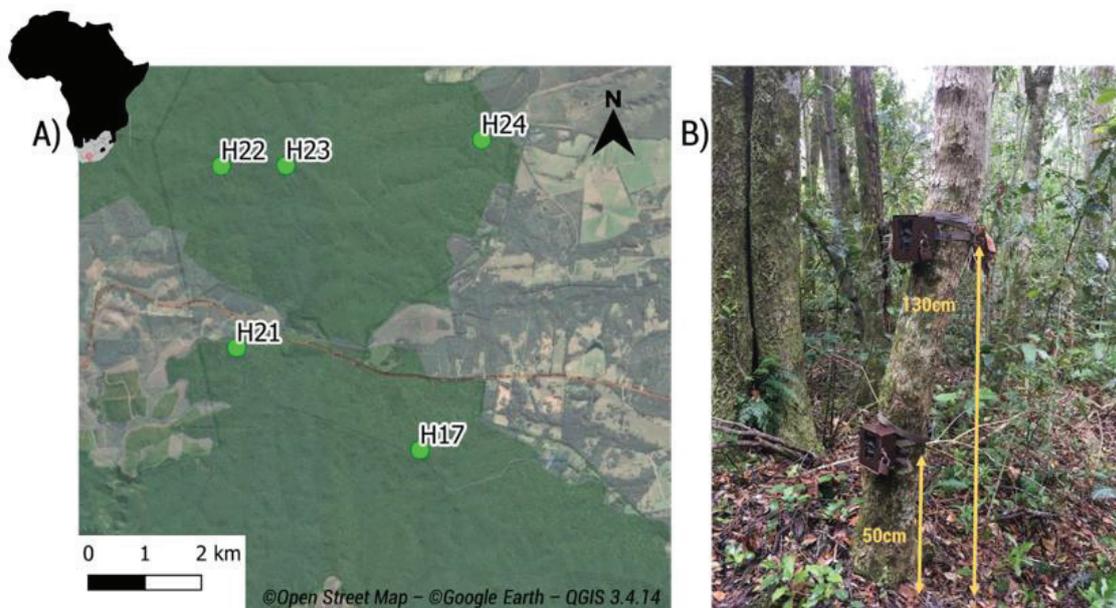
## References

- Alexander, R.M., 2004, 'Bipedal animals, and their differences from humans', *Journal of Anatomy* 204(5), 321–330. <https://doi.org/10.1111/j.0021-8782.2004.00289.x>
- Anile, S. & Devillard, S., 2016, 'Study design and body mass influence RAIs from camera trap studies: Evidence from the Felidae', *Animal Conservation* 19(1), 35–45. <https://doi.org/10.1111/acv.12214>
- Apps, P. & McNutt, J.W., 2018, 'Are camera traps fit for purpose? A rigorous, reproducible and realistic test of camera trap performance', *African Journal of Ecology* 56(4), 710–720. <https://doi.org/10.1111/aje.12573>
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T. et al., 2015, 'REVIEW: Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes', *Journal of Applied Ecology* 52(3), 675–685. <https://doi.org/10.1111/1365-2664.12432>
- Child, F.M., Roxburgh, L., Do Linh San, E., Raimondo, D. & Davies-Mostert, H.T., 2016, The red list of mammals of South Africa, Swaziland and Lesotho, South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, viewed 14 March 2022, from [www.ewt.org.za](http://www.ewt.org.za).
- Edwards, M.A., Derocher, A.E., Hobson, K.A., Branigan, M. & Nagy, J.A., 2011, 'Fast carnivores and slow herbivores: Differential foraging strategies among grizzly bears in the Canadian Arctic', *Oecologia* 165(4), 877–889. <https://doi.org/10.1007/s00442-010-1869-9>
- Edwards, S., Cooper, S., Uiseb, K., Hayward, M., Wachter, B. & Melzheimer, J., 2018, 'Making the most of by-catch data: Assessing the feasibility of utilising non-target camera trap data for occupancy modelling of a large felid', *African Journal of Ecology* 56(4), 885–894. <https://doi.org/10.1111/aje.12511>
- Findlay, M.A., Briers, R.A. & White, P.J.C., 2020, 'Component processes of detection probability in camera-trap studies: Understanding the occurrence of false negatives', *Mammal Research* 65(3), 167–180. <https://doi.org/10.1007/s13364-020-00478-y>
- Fox, J. & Weisberg, S., 2019, *An {R} companion to applied regression*, 3rd edn., Sage, Thousand Oaks, CA.
- Hofmeester, T.R., Cromsigt, J.P.G.M., Odden, J., Andrén, H., Kindberg, J. & Linnell, J.D.C., 2019, 'Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison', *Ecology and Evolution* 9(4), 2320–2336. <https://doi.org/10.1002/ece3.4878>
- Hofmeester, T.R., Young, S., Juthberg, S., Singh, N.J., Widemo, F., Andrén, H. et al., 2020, 'Using by-catch data from wildlife surveys to quantify climatic parameters and timing of phenology for plants and animals using camera traps', *Remote Sensing in Ecology and Conservation* 6(2), 129–140. <https://doi.org/10.1002/rse2.136>
- Jacobs, C.E. & Ausband, D.E., 2018, 'An evaluation of camera trap performance – What are we missing and does deployment height matter?', *Remote Sensing in Ecology and Conservation* 4(4), 352–360. <https://doi.org/10.1002/rse2.81>
- Kolowski, J.M., Oley, J. & McShea, W.J., 2021, 'High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time', *Ecosphere* 12(2), e03350. <https://doi.org/10.1002/ecs2.3350>
- Lüdecke, D., 2018, 'ggeffects: Tidy data frames of marginal effects from regression models', *Journal of Open Source Software* 3(26), 772. <https://doi.org/10.21105/joss.00772>

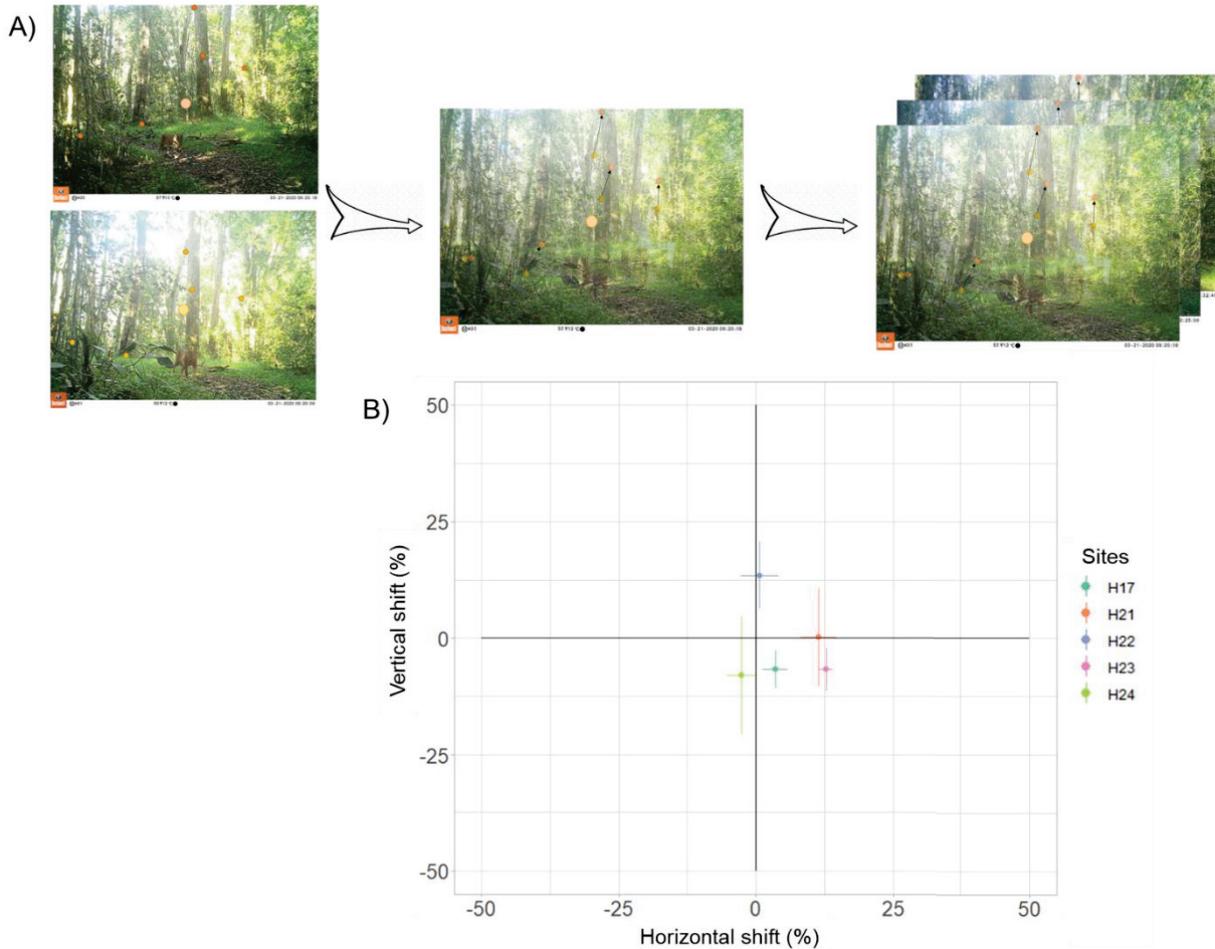
- Mazzamuto, M.V., Lo Valvo, M. & Anile, S., 2019, 'The value of by-catch data: How species-specific surveys can serve non-target species', *European Journal of Wildlife Research* 65(5), 68. <https://doi.org/10.1007/s10344-019-1310-6>
- McIntyre, T., Majelantle, T.L., Slip, D.J. & Harcourt, R.G., 2020, 'Quantifying imperfect camera-trap detection probabilities: Implications for density modelling', *Wildlife Research* 47(2), 177–185. <https://doi.org/10.1071/WR19040>
- Meek, P., Ballard, G., Fleming, P. & Falzon, G., 2016a, 'Are we getting the full picture? Animal responses to camera traps and implications for predator studies', *Ecology and Evolution* 6(10), 3216–3225. <https://doi.org/10.1002/ece3.2111>
- Meek, P.D., Ballard, G.A. & Falzon, G., 2016b, 'The higher you go the less you will know: Placing camera traps high to avoid theft will affect detection', *Remote Sensing in Ecology and Conservation* 2(4), 204–211. <https://doi.org/10.1002/rse2.28>
- Moolman, L., De Morney, M.A., Ferreira, S.M., Ganswindt, A., Poole, J.H. & Kerley, G.I.H., 2019, 'And then there was one: A camera trap survey of the declining population of African elephants in Knysna, South Africa', *African Journal of Wildlife Research* 49(1), 16–26. <https://doi.org/10.3957/056.049.0016>
- Palencia, P., Vicente, J., Soriguer, R.C. & Acevedo, P., 2021, 'Towards a best-practices guide for camera trapping: Assessing differences among camera trap models and settings under field conditions', *Journal of Zoology* 316(3), 197–208. <https://doi.org/10.1111/jzo.12945>
- Pardo, L.E., Bombaci, S.P., Huebner, S., Somers, M.J., Fritz, H., Downs, C. et al., 2021, 'Snapshot Safari: A large-scale collaborative to monitor Africa's remarkable biodiversity', *South African Journal of Science* 117(1/2). <https://doi.org/10.17159/sajs.2021/8134>
- R Core Team, 2020, R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna.
- Royle, J.A., 2011, 'Camera trap in ecology', in A.F. O'Connell, J.D. Nichols & K.U. Karanth (eds.) *Camera traps in animal ecology*, pp. 163–190, Springer, Tokyo.
- Soni, A., Mishra, S., Santra, A., Khune, V., Pathak, R., Dubey, A. et al., 2020, 'Position of centre of gravity in different species: A review', *Journal of Entomology and Zoology Studies* 8(1), 496–499.
- Swann, D.E., Hass, C.C., Dalton, D.C. & Wolf, S.A., 2004, 'Infrared-triggered cameras for detecting wildlife: An evaluation and review', *Wildlife Society Bulletin* 32(2), 357–365. [https://doi.org/10.2193/0091-7648\(2004\)32\[357:ICFDWA\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2004)32[357:ICFDWA]2.0.CO;2)
- Tobler, M.W., 2007, Camera base version 1.3, viewed 10 March 2021, from <http://www.atrrium-biodiversity.org/tools/camerabase/>.
- Venables, W.N. & Ripley, B., 2002, *Modern applied statistics with S*, 4th edn., Springer, New York, NY.
- Wickham, H., 2016, *ggplot2: Elegant graphics for data analysis*, Springer-Verlag, New York, NY.

## Supplementary material for the manuscript 1: Height related detection biases in camera trap surveys: insights for combining data sets

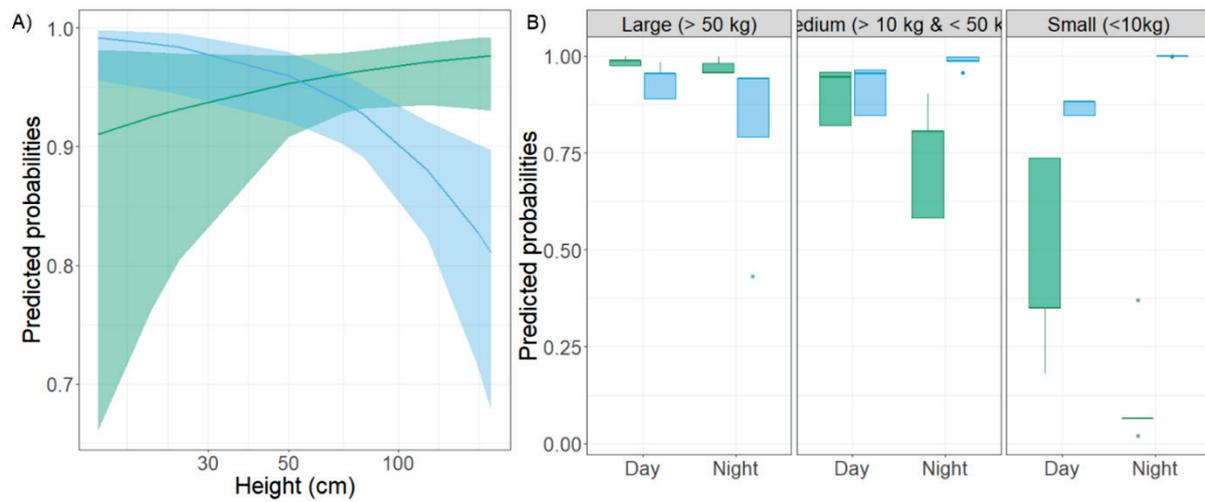
### Figures



**FIGURE1 - A1:** A) Location of the five sites in the Harkerville forest, Garden Route National Park, Western Cape, South Africa; B) Position of the high and low cameras on a tree.



**FIGURE 2 -A1:** A) For each site, we compared a photograph of the same event taken by the cameras at 130 cm and one taken by the cameras at 50 cm. We selected five similar points on each photograph. Then we measured the horizontal and vertical shift from the high camera compared to the low camera. We repeated the methods with three different events. We calculated a percentage of shift using the size of the photograph as the value of reference. B) We then plotted the percentage of mean and standard deviation for each site, corresponding to the shift in direction between low and high cameras. This shows a small shift between the two heights of the cameras, mostly on the horizontal axis.



**FIGURE 3 – A1:** Predicted probabilities of detection of the best generalised linear model as a function of A) the height of the species by treatment and B) the weight of the species, sorted by treatment and day/night photographs.

## Tables

**TABLE1 - A1:** Species detected on camera traps in the Harkerville Forest, Garden Route National Park, Western Cape, South Africa, and their characteristics.

<b>Mammal species and human related events</b>	<b>Height (cm)</b>	<b>Weight (kg)</b>	<b>Total number of detection</b>	<b>Camera height</b>	<b>Number of detection</b>
<b>Leopard</b>	70	55	9	High	9
				Low	9
<b>Bushbuck</b>	70	54	146	High	140
				Low	136
<b>Bushpig</b>	80	65	31	High	29
				Low	30
<b>Baboon</b>	80	24	26	High	26
				Low	25
<b>Vervet monkey</b>	50	5	6	High	4
				Low	6
<b>Porcupine</b>	70	17	19	High	13
				Low	19
<b>Caracal</b>	50	13	6	High	6
				Low	4
<b>South African large-spotted genet</b>	21	1.6	61	High	6
				Low	60
<b>Cape grey mongoose</b>	15	0.8	2	High	0
				Low	2
<b>Honey badger</b>	25	12	30	High	24
				Low	29
<b>Dogs without human</b>	50	30	10	High	9
				Low	10
<b>Dogs with human</b>	50	30	11	High	11
				Low	11
<b>Human</b>	165	70	147	High	146
				Low	124
<b>Motorcycle</b>	165	250	35	High	35
				Low	35
<b>Vehicle</b>	180	1200	5	High	5
				Low	5

Source: Child, F.M., Roxburgh, L., Do Linh San, E., Raimondo, D. & Davies-Mostert, H.T., 2016, The red list of mammals of South Africa, Swaziland and Lesotho, South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, viewed from [www.ewt.org.za](http://www.ewt.org.za)

**TABLE2 - A1:** Results of the A) step AIC procedure and B) statistical model relating species' detection with camera height.

**A) Results of the step AIC procedure (variables and/or interactions removed at each step):**

Step	df	Deviance Residual	df Residual	Deviance	AIC	
1	-		1068	436.4	476.4	
2	- Height:weight:period photo:treatment	1	0.24047	1069	436.7	474.7
3	- Height: weight:treatment	1	0.99029	1070	437.8	473.7
4	- Height:period photo:treatment	1	1.00914	1071	438.7	472.7
5	- Height:weight:period photo	1	0.92221	1072	439.6	471.6
6	- Height:weight	1	0.42018	1073	440.0	470.0
7	- Site	4	6.55267	1074	446.6	468.6
8	- Height:period photo	1	1.06879	1078	447.6	467.6

Note: Initial Model:  $detection \sim Site + (height * weight * period\ photo) * treatment$ .

Final Model:  $detection \sim height + weight + period\ photo + treatment + weight:period\ photo + height:treatment + weight:treatment + period\ photo:treatment + weight:period\ photo:treatment$ .

**B) Results of the glm for the best model:**

	Estimate	Std. Error	P
(Intercept)	-2.8419	1.5272	.
Height	1.3195	1.1725	NS
Weight	2.3369	0.7118	**
Night photo	-2.2510	0.8927	*
Low treatment	8.5848	2.1905	***
Weight:night photo	0.9782	0.6962	NS
Height:low treatment	-4.4112	1.5851	**
Weight:low treatment	-0.6010	0.9768	NS
Night photo:low treatment	10.0768	3.7985	**
Weight:night photo:low treatment	-5.6293	2.1676	**

P: NS > 0.1 > . > 0.05 > \* > 0.01 > \*\* > 0.001 > \*\*\*.

**TABLE3 – A1: Results of the independent McNemar tests.**

<b>Species</b>	<b>p-value</b>	<b>P</b>
Human	7,10E-06	***
Bushbuck	0,317	NS
Caracal	0,157	NS
Genet	5,35E-13	***
Ratel	0,059	.
Bushpig	0,564	NS
Baboon	0,317	NS
Vervet monkey	0,157	NS
Dogs with people	NA	
Porcupine	0,014	*
Dogs without people	0,317	NS
Motorcycle	NA	
Vehicle	NA	
Leopard	NA	
Mongoose	0,157	NS

## Manuscript 2

# Spatio-temporal overlap between African mammals and humans in a multifunctional landscape: insights on the concept of anthropodependence

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## Abstract

Terrestrial ecosystems are being transformed by humans at an alarming rate jeopardizing most vertebrate species. To survive in ever-expanding human-dominated landscapes, mammal species need to be able to adapt to various anthropogenic changes. As mammal species are relatively diverse in their life history traits, they are expected to show different behaviors in response to the modification of their habitats. Here, we assessed the spatio-temporal use of the multifunctional landscapes of the Garden Route Biosphere Reserve, South Africa by 14 medium to large mammal species (>500 g). Using 75 camera traps for one year, we estimated their habitat use in different land cover types (indigenous forest and cultivated areas) and levels of human disturbances (distance from infrastructure and density of roads), in two contrasting seasons (winter and summer), using occupancy modelling. We also assessed whether the protection status of the sites affected species habitat use. We then calculated their temporal overlap with human activity in areas with low and high road density, and distance from human infrastructure to assess sensitivity to human presence and associated disturbances. Our results showed the diversity of strategies developed by mammals to occupy human-modified habitats, with species spread along gradients of naturalness and human disturbances, suggesting different cost-benefits, as hypothesized by the anthropodependence framework. Site protection status did not matter much, and was partially confounded with natural forest effects. While nine out of 11 species reduced their temporal overlap activities with human activity in areas with high road density, the changes associated with distance to infrastructure concerned few species. Combining occupancy and temporal responses to human disturbances were useful to better understand species responses to anthropogenic features. Our study provides examples of how mammals persist in multifunctional landscapes and helps inform future land planning and research priorities.

**Key words:** Camera trap, occupancy, activity pattern, wildlife, animal behaviour, human disturbance, anthropogenic landscapes, conservation

## 1 | Introduction

Transformations of terrestrial ecosystems by human activities are occurring at a fast pace and human footprint, a measure of these transformations, has been detected on 75% of continental lands (Ellis et al. 2010; Venter et al. 2016c). Biodiversity is facing unprecedented declines and a quarter of all species are considered threatened by extinction (Dirzo et al. 2014; Diaz 2019). Mammals are particularly affected by habitat alteration, overexploitation, climate change, pollution and invasive species (Fischer & Lindenmayer 2007; Atwood et al. 2020). To counteract land transformation and preserve the remaining suitable habitats for wildlife, 16% of the land is protected in the world (UNEP-WCMC et al. 2020). The effectiveness of these areas can vary and does not necessarily protect the suitable habitats for all species, such as species occurring at low-densities with large home ranges (Cazalis et al. 2020; Maxwell et al. 2020; Scholte et al. 2021; Gatiso et al. 2022). To improve effectiveness, connectivity between various protected areas appear crucial for preserving animal movement (Cumming et al. 2015; Brennan et al. 2022). Indeed, a reduction of 50% of human footprint in human-dominated areas would reduce isolation of protected areas by 28% (Brennan et al. 2022). It seems essential to redesign how humans share space with wildlife to help reduce biodiversity loss (Obura et al. 2021). Creating patches favorable habitats could offer a refuge for species and can effectively complement protected areas (Shumba et al. 2020; Taylor et al. 2021; Leighton et al. 2022; Woodgate et al. 2023).

The scales at which humans affect mammal species can vary greatly thus impacting their spatial, temporal and dietary niche (Nickel et al. 2020; Sévêque et al. 2020; Suraci et al. 2021; Van Scoyoc et al. 2023). Human encounters are short events which might be easy to avoid for animals, whereas human presence associated with land use activities (e.g. farming, hiking, hunting) may impose longer-lasting effects, and human footprint (habitat fragmentation, urbanization) creates more permanent constraints on mammal ecology (Moleón & Sánchez-Zapata 2023). Although human activities are often documented to be negative, anthropogenic landscapes can benefit some species by providing new food resources (e.g. prey for wild carnivores), concentrating food resources or offering new hunting strategies for carnivores (Yirga et al. 2012; Drouilly et al. 2018; Fleming & Bateman 2018). Living in a human-dominated landscape might be an advantage for species, which could spend less time foraging and more time resting or socialising (Gaynor et al. 2018). Food availability, disturbance or biological rhythms can be seasonal and influence mammal habitat use (O'Connell et al. 2006; Kays et al. 2020; Sévêque et al. 2020). Some human activities, such as agricultural practices, daily or recreational activities (e.g. holidays), can be predictable and therefore be avoided by animals (Moleón & Sánchez-Zapata 2023). For example, some species change their pattern of temporal activity to avoid human encounters and become more nocturnal (Gaynor et al. 2018). To understand wild species responses to anthropogenic features, Hulme-Beaman et al. (2016) proposed a framework to define four types of wildlife populations based on home-range overlap and consumption of anthropogenic resources. Anthropodependent and synanthropic species use the same spatial niche as humans, whereas anthropophilic and anthropophobic species rely on natural habitats. Anthropodependent and anthropophilic species significantly consume human food resources (Hulme-Beaman et al. 2016). Mammals constitute a diverse taxonomic group, occupy a wide range of habitats, have various positions in trophic levels, and are often

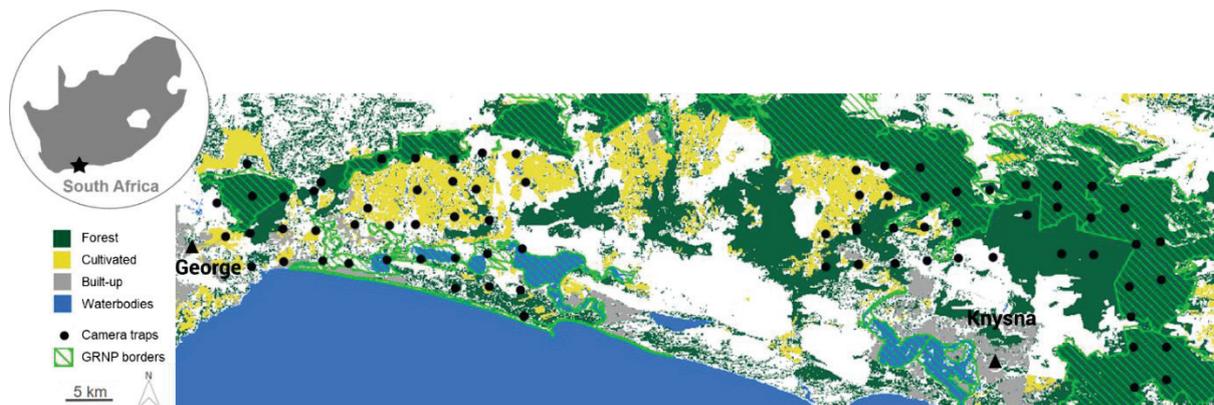
vulnerable to habitat fragmentation. We, therefore, believe that they are good indicators of ecosystem perturbations and are likely to display a diversity of responses.

In this study, we used camera trap (CT) data to investigate spatial and temporal responses of mammals to anthropogenic disturbances in the Garden Route Biosphere Reserve (GRBR) human-dominated landscape, in South Africa, in two contrasting seasons, summer and winter. The Garden Route National Park (GRNP) is a fragmented open-access primary protected area of the GRBR, embedded in a variety of human-dominated landscapes and productive activities. The GRNP hosts a diversity of recreational activities and is well used by humans in search of outdoor experiences (Roux et al., 2020). Given the present trend in residential and farming development in the area, more knowledge is needed to manage the impact of the landscape dynamics on mammal habitat use and temporal activities (Western Cape Government 2019). The aim of our study was to understand the variation in the spatial, seasonal and temporal niches occupied by mammals. We limited our assessment of Hulme-Beaman et al. (2016) conceptual framework to the spatial and temporal niche overlap between humans and mammals, *i.e.* the habitat use axis and not the resource use axis. Human presence and landscape transformation can have various and sometimes opposite effects on mammals (Nickel et al. 2020; Sévêque et al. 2020; Suraci et al. 2021), but studies mostly highlighted the effect of landscape transformation, suggesting that species are often capable of mitigating the impact of human presence by avoiding them (Gaynor et al. 2018; Suraci et al. 2021). Here we tested the impact of site protection status on the presence of species. We then used landscape metrics (*i.e.* forest and cultivated areas), as well as density of roads and distance to infrastructure as proxies of structural sources of disturbances, to assess species occupancy. We completed the study by assessing the temporal overlap between mammals and human activities, in areas with low and high human disturbances, to highlight potential and direct impacts on mammals (Van Scoyoc et al. 2023). We expected that species would not only respond differently to landscape features but could also be classified on a gradient of tolerance to human disturbance (direct or indirect). For instance, we expected that diurnal species would change their peak of activity to avoid humans encounter if they are sensitive to humans, if they consume human resources or use human-dominated areas, to avoid being detected. We expected that some species might exhibit an increase in human landscape use during a certain season, to seek resources when natural food sources become scarcer. We also expected shy species to avoid seasonal human peaks of activity such as tourist holiday periods, or species exhibiting an increase in human landscape features when anthropogenic resources are available and easy to access. Our study thus offers a baseline information on mammals' spatial and temporal niche adjustments in human-dominated habitats to test and expand on existing conceptual frameworks which can help inform future management and research priorities.

## 2 | Materials and methods

### 2.1 | Study area

The study was carried out within the GRBR, between the town of George and Knysna, in the Western Cape, on the south-eastern coast of South Africa (Figure 1). The GRBR is a multifunctional landscape, including agriculture, peri-urban and conservation areas. Since 1930, the number of suburbs and residences in the GRBR has increased dramatically (Crisp 2015). The population was over 620,000 in 2019 and is expected to increase in the future (Western Cape Government 2019). The GRNP, managed by South African National Parks (SANParks), was established in 2009 with the primary objective of protecting the indigenous Afrotropical forest (Baard et al. 2015). The GRNP includes a variety of natural vegetation such as Afrotropical forests, fynbos, thicket and wetlands (Baard et al. 2015; SANParks 2020). The park is fragmented by diverse agricultural use with extensive systems (crops and dairy farming), exotic pine plantations, residential, informal and urban areas and is interspersed with a vast road network (Department of Forestry, Fisheries and the Environment 2020), *i.e.* a landscape mosaic with natural and managed green spaces. The unfenced National Park is open-access for visitors, who can practice outdoor activities such as mountain biking or hiking (Roux et al. 2020). Outside formally protected areas, Critical Biodiversity Areas (CBAs), identified in the Western Cape Biodiversity Spatial Plan (2017), from a network of non-formal conservation areas identified and designated to meet targets for ecosystems, species and ecological processes with the least conflict with other activities. They often protect sensitive micro-catchments, the GRNP buffer area, and possible wildlife corridors. The climate is considered as temperate, with summer running from November to March, and winter from June to August. They are the most contrasted periods in terms of temperatures, ranging from 15 to 25°C in summer and 7 to 19°C in winter (Baard et al. 2015).



**FIGURE 1** Map of the study area, in the Garden Route Biosphere Reserve, South Africa, represented by the black star. Location of the camera traps are represented by black dots. The GRNP borders are drawn in light green. The forest habitats are colored in dark green, the agriculture areas are in yellow and water is in blue. The land covers are sourced from the SA National Land Cover Datasets (Department of Forestry, Fisheries and the Environment 2020).

### 2.2 | Data collection and processing

We used a single camera trap (CT) per site to detect terrestrial mammals across 75 sites. As part of the Snapshot Safari Project (Pardo et al. 2021), CTs set-up follow a standardized protocol. CTs were set-up as close as possible to the center of a regular grid of 5 km<sup>2</sup>, resulting in a CT spacing of about 2.3km. We used: 33 Bushnell Trophy Cam HD Aggressor and 42 SPYPOINT Force-Dark CTs. When possible, they were set on game trails and fixed at height of 50 cm (**manuscript 1**), mainly on trees, to detect medium to large mammals (mean height of the mammal species of the area = 50 cm, range from 15 to 80 cm), and were secured with steel cases. Each CT was programmed to take a series of three images when triggered with one-minute delay between each trigger. CTs were checked every two to three months to change the batteries and SD cards. The survey ran continuously from the 2nd of February 2021 to the 20th of May 2022. Four CTs were stolen during the survey: one before the first service (in May 2021) and three others between February 2022 and May 2022. We had 75 CTs running at the same time but eight of them were moved for technical reasons, resulting in a total of 83 different sites. The photographs were manually tagged, firstly by using digiKam (digiKam team 2001), then with the online software TrapTagger (Osner 2022). After removing empty photographs, all images were identified. Vehicles, motorcycle, bicycle or passing humans were considered as a human detection.

## 2.3 | Data analysis

### 2.3.1 | Occupancy modelling

We performed a single species, single-season, occupancy modelling to study the effect of anthropogenic features on the occupancy of mammals (MacKenzie et al. 2017). Occupancy models use a temporal replicate of detection and non-detection of a species at a given site to produce a corrected estimate of the probability of occupancy  $\Psi$ , *i.e.* that at least one individual of a species occupies a given site, and the probability of detection  $p$ , which is the probability of detecting the species at a site, given that the site is occupied (MacKenzie et al. 2017). They estimate the probability of occupancy,  $\psi$ , and detection  $p$  (MacKenzie et al. 2002). We divided our dataset into two seasons of three months each: summer (November-January) and winter (June-August), to compare the responses of the species between two contrasting seasons, while ensuring the assumption of population closure required in occupancy analysis (MacKenzie et al. 2017). We created a detection matrix for each species, grouped by 7 days, resulting in 16 survey occasions (“detectionHistory” function, “camtrapR” package), to have enough detections for rare species (Niedballa et al. 2016). Each species used for the modelling had at least 12 observations per season (Table S1). As some species with wide home ranges may violate the spatial independence assumption, we will refer to habitat use and not occupancy.

#### 2.3.1.1 | Estimating the probability of detection $p$

To make inferences about factors driving habitat use by species, we first controlled for variables which could explain heterogeneity in the detection of the species between the sites: (1) the visibility in front of the CT, measured as the effective distance at which CT detected a human; (2) the height of CT set-up from the ground as we sometimes had to adjust the height above the 50cm target height; and (3) the location of the CT, by classifying whether on a road, on a trail, on a game trail or outside of any identified trail. As visibility slightly changed over

time (growing vegetation), we recorded this information, every time we checked the CTs. The probability of detection was given by:  $\text{logit}(p_{ij}) = \beta_{0jk} + \beta_1 \text{Height}_{ij} + \beta_2 \text{Visibility}_{ij} + \beta_3 \text{Trail}_{ij}$

### 2.3.1.2 | Estimating the probability of occupancy $\psi$

As site protection status may play a role in the way species perceive humans as disturbances, we first tested the effect of the protection status on species habitat use following the method presented in the **supplementary material for the manuscript 2** (Supplementary Methods - Occupancy analyses). We tested four occupancy landscapes metrics, which could have affected the habitat use of the studied species. We calculated the percentage of forest cover and cultivated areas around each site in a buffer of 500 m around the CTs, using the 2020 SA National Land Cover Datasets (18 m resolution; Department of Forestry, Fisheries and the Environment 2020). Cultivated areas included pastures, orchards, and permanent and temporary crops. We respectively named the variables forest and cultivated. We calculated the length of roads in the same 500 m buffer to the potential disturbance associated with human footprint ('st\_intersection' and 'st\_length' function, 'sf' package; Pebesma 2018), and will refer to this variable as road density. Finally, we manually marked anthropogenic infrastructures (*i.e.*, building and houses) around each CT on QGIS, using Google satellite images from 2021, and calculated the distance to the closest infrastructure. We used a logarithm transformation to get a more uniformly distributed gradient, that we named distance to infrastructure. Sites with a high percentage of forest, far from human infrastructure and with relatively little cultivated areas corresponded to the GRNP (Figure S1), hence highly redundant with our landscapes metrics. We tested the correlation between each of the candidate variables ('cor' function, 'stats' package), and found no correlation (Pearson correlation coefficient <0.7, Figure S2 and S3). Detection and occupancy variables were scaled ('scale' function, 'base' package), to allow for direct comparison.

For each species, we ran a model per season, including all four previously described variables in the model. The same occupancy model was used for each species to be able to compare their responses to each variable. We fitted linear and quadratic terms to test for potential nonlinear effects of the distance to infrastructure and road density on species responses, as suggested by previous research (Suraci et al. 2021). Scaling variables allowed us to interpret separately linear and quadratic terms (Schielzeth 2010). Hence the probability of occupancy was given by the following function:  $\text{logit}(\Psi_i) = \alpha_0 + \alpha_1 \text{Cultivated}_i + \alpha_2 \text{Forest}_i + \alpha_3 \text{Infrastructures}_i + \alpha_4 \text{Infrastructures}_i^2 + \alpha_5 \text{Roads}_i + \alpha_6 \text{Roads}_i^2$

We analyzed all models in a Bayesian framework using the Jags programming language ('rjags' package ; Martyn Plummer 2022). For each model, we ran three Hamiltonian Monte Carlo (HMC) chains with 30,000 iterations, and used a burn in of 20,000 and a thinning rate of 10 (Kéry & Schaub 2012). We chose priors with a mean of 0 and standard deviation of 1, with a normal distribution for all random starting values (Gelman et al. 2008). We visually confirmed convergence of HMC chains by inspecting the trace plots and confirming with the Gelman–Rubin statistic ('R-hat' values <1.1 for all parameters; Table S2 ; Gelman 2006). We tested model fit using Bayesian p-values, which compare observed and expected data, using Freeman–Tukey statistic test (Conn et al. 2018). We detected a fit between  $0.33 \leq p \leq 0.66$  (Table S3). We calculated the Bayesian information criterion (BIC ; Table S4). Using the Bayesian posterior distribution of the coefficient estimate, we determine whether variables had

a positive or negative effect on site occupancy for a given species. We considered variables to have a significant effect when the 95% credible interval (CI) of the estimate did not overlap zero.

### 2.3.2 | Temporal overlap

To study the overlap of temporal niche between mammals and humans we calculated their temporal activity patterns in sites with different protection status as discussed in the **supplementary material for the manuscript 2** (Supplementary Methods - Temporal analyses). We then calculated temporal overlap between humans and mammals in areas with high road density than areas with low road density, that we assumed were respectively associated with a higher and lower risk of encountering humans. We considered road length in the 500m buffer > 750m to be high and above to be low (Figure S2). Human activity regrouped the detection of humans, vehicles and bicycles. We calculated the temporal activity of each species and the overlap with humans in areas with high and low road density, to assess whether they were using the same temporal niche as humans. We calculated the  $\Delta 4$  overlap coefficient ('overlapEst' function, 'overlap' package), which represented the proportion of overlap between the two activity curves. Zero means that there was no overlap and 1 that the two curves overlapped completely (Ridout & Linkie 2009). To compare the observed value with the distribution of the null hypothesis, we randomly simulated 1000 temporal activity curves for each mammal ('resample' function, 'overlap' package) and estimated the 95% confidence interval for each overlap value as done by Karanth et al. (2017). Finally, to evaluate the similarity of mammal activity between areas with high and low road density, we calculated the observed overlap of the same species between the two areas. It provides information at two levels (1) a modification of the temporal niche in risky areas, illustrated by a change of overlap with humans between quiet and busy areas and (2) behavioral responses associated with the direct risk avoidance, *i.e.* avoidance of humans, indicated by a temporal overlap value outside the 95% expected CI. We repeated the same procedure to calculate temporal activity patterns in areas close to human infrastructure compared to far ones, which we predicted to also be associated respectively with a higher and lower risk of encountering humans. We considered human infrastructure to be close if < 1200 m and far above this value. Species considered for the analyses had at least 20 observations (Figure S2, Table S5 and S6). As recommended by Peral et al. (2022), we did not filter the data for independence.

All the analyses were performed on R 4.2.2 (R Core Team 2020), and QGIS v3.4.14 (QGIS Association 2022). We used the package ggplot2 for graphical representations (Wickham 2016).

### 3 | Results

Our sampling effort corresponded to 29,392 trap nights, with a total of 253,179 photographs, of which 40,235 corresponded to wild mammal species (44%), 41% to human activities (humans, vehicles, domestic animals), 12% to birds and 2% to rodents. The 1% left corresponded to other species such as reptiles and insects. A total of 15 wild mammal species were detected on the CTs, from eight families and four orders (Table 1). The order Artiodactyla was represented by four species, Carnivora by eight species, Primates by two and Rodentia by one (Table 2). The bushbuck (*Tragelaphus scriptus*) was the most detected species with 23,885 photographs (59% of the photos) on 79 different sites (95% of the sites). The chacma baboon (*Papio ursinus*; 11%), Cape porcupine (*Hystrix africaeaustralis*, 7%), large-spotted genet (*Genetta tigrina*; 6%) and bushpig (*Potamochoerus larvatus*; 6%) represented the next four photographed species. The Cape leopard (*Panthera pardus*) and the large grey mongoose (*Herpestes pulverulentus*) were rare and we recorded less than 130 photographs (<1%). The Cape clawless otter (*Aonyx capensis*) was only detected twelve times on three sites, and because of its few detections, we did not run occupancy models for this species (Table 1).

**TABLE 1** Detected species and number of photographs and percentage of occupied sites on the 75 sites.

Common name		Scientific name	Number of photographs	Percentage sites
Bushbuck		<i>Tragelaphus scriptus</i>	23885	95%
Cape porcupine		<i>Hystrix africaeaustralis</i>	2859	53%
South African large-spotted genet		<i>Genetta tigrina</i>	2286	86%
Chacma baboon		<i>Papio ursinus</i>	4243	52%
Bushpig		<i>Potamochoerus larvatus</i>	2390	77%
Vervet monkey		<i>Cercopithecus pygerythrus</i>	1732	36%
Blue duiker		<i>Philantomba monticola</i>	1047	25%
Water mongoose		<i>Atilax paludinosus</i>	352	41%
Cape grey mongoose		<i>Herpestes pulverulentus</i>	313	34%
Caracal		<i>Caracal caracal</i>	395	40%
Honey badger		<i>Mellivora capensis</i>	252	46%
Cape grysbok		<i>Raphicerus melanotis</i>	254	12%
Leopard		<i>Panthera pardus</i>	123	18%
Large grey mongoose		<i>Herpestes ichneumon</i>	104	16%

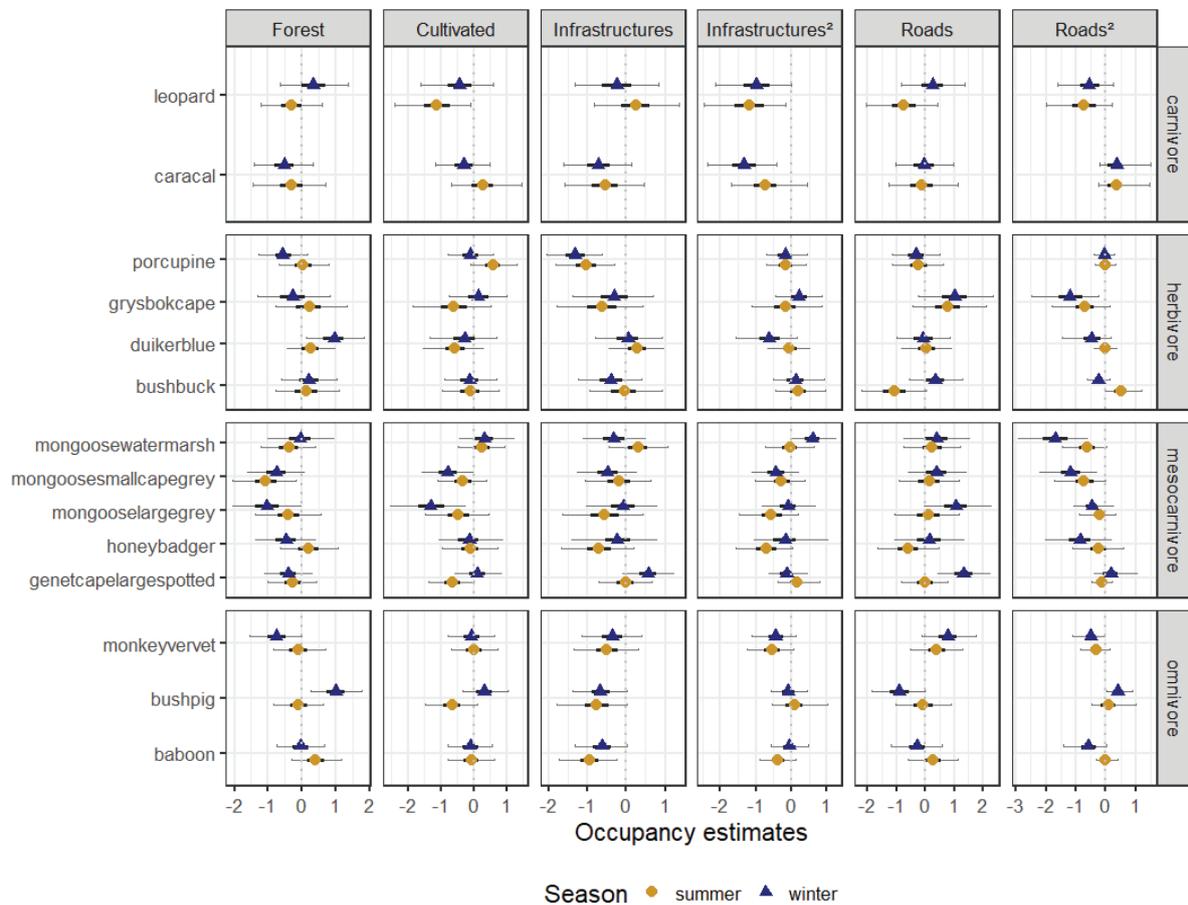
### 3.1 | Effect of landscape variables on species habitat use

Although mammals responded differently to the protection status, they seem to overall mainly occupy CBAs (Figure S4). However, it does not seem to be the only factor influencing mammals' use of human-dominated mosaic landscapes (Figure S4). The occupancy models based on landscape metrics highlighted few estimates with 95% CI not overlapping zero, on which we focused (Figure 2). The blue duiker (*Philantomba monticola*), bushpig, leopard, large-spotted genet, Cape (*Herpestes pulverulentus*) and large grey mongoose species occupancy probabilities were primarily associated with landscape features (forest or cultivated), while others (bushpig, leopard, large-spotted genet, caracal, baboon, vervet monkey *Cercopithecus pygerythrus*, Cape grysbok *Raphicerus melanotis*, Cape porcupine, Cape and water mongoose *Atilax paludinosus*) with human disturbances (distance to infrastructure or road density), and with seasonality.

The blue duiker and the bushpig were mostly detected in forest areas in winter (respectively  $\alpha = 0.96$ , [95% CI =0.14;1.86] and  $\alpha = 1.01$ , [95% CI =0.28;1.78]). In summer, the trend was the same for the blue duiker, but the effect for the bushpig was negative. The Cape grey mongoose, in summer and the large grey mongoose in winter were less detected in forest areas (respectively  $\alpha = -1.07$ , [95% CI = -2.05; -0.18] and  $\alpha = -1.03$ , [95% CI = -2.05; -0.05]) and the trend was the same for the Cape grey mongoose in winter, and for the large grey mongoose in summer (Figures 2 and S5). Leopards and large-spotted genets were less detected cultivated areas in summer (respectively  $\alpha = -1.14$ , [95% CI =-2.40; -0.1] and  $\alpha = -0.66$ , [95% CI =-1.36; 0]). The Cape grey mongoose and the large grey mongoose were less detected in cultivated areas (respectively  $\alpha = -0.79$ , [95% CI = -1.58; -0.02] and  $\alpha = -1.31$ , [95% CI = -2.55; -0.26]) in winter and the trends were similar in summer (Figures 2 and S5).

The magnitude and direction of the effect of distance to infrastructure and road density varied between species (Figures 2 and S5). Porcupines and baboons were both attracted to human infrastructure in all seasons ( $\alpha = -1.03$ , [95% CI =-1.82; -0.3] in summer and  $\alpha = -1.31$ , [95% CI =-2.03; -0.62] in winter;  $\alpha = -0.95$ , [95% CI =-1.73; -0.23] in summer and  $\alpha = -0.62$ , [50% CI = -0.85, -0.38] in winter respectively). There was a nonlinear effect for the leopard and the caracal (Figures 2 and S5). The effect of distance to infrastructure showed a peak at intermediate value for the leopard at both seasons ( $\alpha = -1.20$ , [95% CI =-2.45; -0.16] in summer and  $\alpha = -0.9998$ , [95% CI =-2.12; -0.01] in winter) and for the caracal in winter ( $\alpha = -1.02$ , [95% CI =-1.91; -0.24]). The optimal value indicated that they rather stay at intermediate distances from infrastructure, corresponding to areas at the interface between protected areas and human-modified habitats (Figures 2 and S5). The large-spotted genet was attracted to areas with a high density of roads in winter ( $\alpha = 1.33$ , [95% CI =0.41; 2.23]), and the effect was negative but not important in summer. Six species had non-linear responses to the road density, four in a negative direction and one in a positive direction (Figures 2 and S5). The effect of roads showed a peak for the Cape grey mongoose at both seasons ( $\alpha = -0.73$ , [95% CI =-1.72; -0.0] in summer and  $\alpha = -1.18$ , [95% CI =-2.21; -0.22] in winter). and in winter for the Cape grysbok ( $\alpha = -1.21$ , [95% CI =-2.46; -0.24]), the vervet monkey ( $\alpha = -0.5$ , [95% CI =-1.13; -0.04]) and the water mongoose ( $\alpha = -1.70$ , [95% CI =-2.91; -0.63]). They had positive estimates for the linear effect, showing an optimum occupancy around intermediate values of road density (Figures 2 and S5). The effect of roads showed a decreasing peak for the bushpig

in winter ( $\alpha = 0.40$ , [95% CI = 0.01; 0.91]), suggesting that they avoided areas with intermediate values of road density and selected areas with low or high road density (Figures 2 and S5).

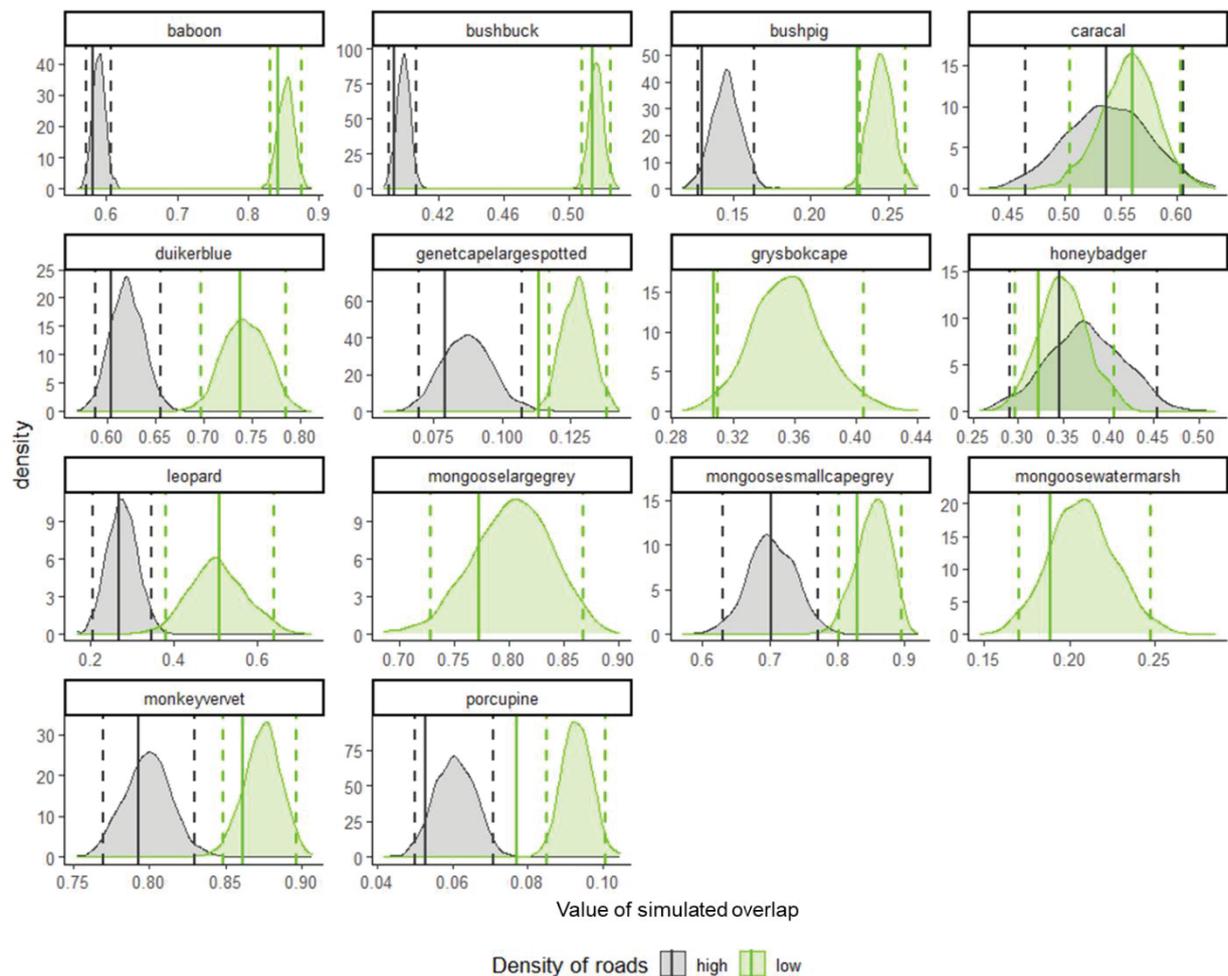


**FIGURE 2** Estimates of the occupancy models for each variable per species and colored per season. Winter is represented by blue triangles and summer in light brown circles. Larger lines represent the 50% Bayesian credible intervals and lighter ones the 95% Bayesian credible intervals. Species are sorted by diet type. The red dotted lines highlight the position of 0 on the x-axis. To the right of the lines, species occurrence has a positive relationship with the variable

### 3.2 | Effect of humans on species temporal activity

Temporal activity, in general, was not influenced by the site protection status of the CTs (Figure S6). All species had an overlap value of temporal activities between areas with low and high road density above 0.7, suggesting a low change in their temporal activities, except for baboon, which had a value of 0.66. However, the grysbok, blue duiker, honey badger, baboon, vervet monkey, large grey and water mongoose showed different activity peaks in areas with high road density suggesting an adjustment of their temporal activity to humans (Figure S7). The baboon, bushbuck, bushpig, blue duiker, genet, leopard, Cape grey mongoose, vervet monkey and porcupine had an overlap with humans lower in areas with high road density than in areas with low road density, showing a modification of their temporal niche in riskier areas and a greater sensitivity to humans in areas where they had more chances of encountering one

(Figure 3). The caracal and the honey badger had the same overlap with human activity in areas with low and high road density (Figure 3). The grysbok, large grey and water mongoose had insufficient data in areas with high road density to run the analysis, suggesting that they are occurring at low densities in these busy areas (Figure 3). Furthermore, the bushpig, genet, grysbok and porcupine showed a higher avoidance of humans than expected in areas with low road density, suggesting a behavioral avoidance associated with the direct risk of human encounters and that they were sensitive to direct human perturbations (Figure 3, Table S7). For all other mammal and human pairs, the observed overlap was within the confidence interval of the distributions simulated in areas with low and high road density (Figure 3, Table S7).



**FIGURE 3** Simulated overlap value between human and mammals in areas with high (in grey) and low road density (in green). The dotted lines represent the 95% credible interval. The solid line represents the true value of occupancy.

Except for the baboon and the honey badger, which had an overlap value of temporal activities between areas with low and high road density of respectively 0.63 and 0.55, all species had a value above 0.7, suggesting a low change in their temporal activities (Table S8). However, the baboon, honey badger and bushpig, had different activity peaks closer than far from infrastructure suggesting that they were responding to the direct presence of humans (Figure S8). Distance to infrastructure seemed to affect the temporal niche of species to a lesser extent, except for the Cape grey mongoose, baboon and genet which had a higher overlap

with humans close to anthropogenic infrastructure (Figure S9). The leopard, grysbok and large grey mongoose, three rare species, did not have enough data in areas far from infrastructure to be able to run the analysis (Figure S9). For all other mammal and human pairs, the observed overlap was within the confidence interval of the distributions generated using the random records in areas close and far from infrastructure (Figure S9). The bushpig, genet, grysbok and porcupine showed a higher avoidance of humans than expected in areas close to infrastructure, suggesting again a short-term behavioral response to avoid the direct risk of human encounter (Figure S9).

## 4 | Discussion

### 4.1 | Spatio-temporal responses of mammals

Our study regrouped the spatial and temporal responses of 14 different mammal species to landscape and human disturbance variables, during two contrasting seasons. A diverse mammal community remained in the multifunctional landscape of the GRBR, supporting the idea that a multifunctional landscape with a mosaic including green spaces (natural and managed), is favorable to maintaining biodiversity. Species appeared to occupy widely CBAs and exhibited idiosyncratic responses to the landscape metrics tested. Four species of carnivores avoided cultivated areas (leopard, large-spotted genet, Cape and large grey mongooses). The blue duiker and the bushpig are two forest specialists (Venter et al. 2016b, 2016a), and were more likely to use forest habitats. Sensitive species such as the blue duiker probably stay in forests of protected areas to avoid risky places (Riley 2006; Ordeñana et al. 2010; Wilmers et al. 2013). Our results highlighted that some of the species occurring in the GRBR occupy different land-uses and showed a tolerance to human disturbances (i.e. density of roads and distance to infrastructures) Distance to human infrastructure and density of roads were not equivalent in their effects on mammals' habitats use as suggested by Suraci et al. (2021), and in our study, species were affected by only one type of disturbance. Two species were attracted by human infrastructure (baboon and porcupine), and two by intermediate distance to human infrastructure (leopard and caracal), corresponding to the interface area between protected and human-dominated areas. One species seemed to use areas with a higher road density more (large-spotted genet), and five had an optimum probability of habitat use around intermediate values of road density; the effect of road density on species occupancy was negative for four (grysbok, vervet monkey, Cape and water mongoose) and positive for one (bushpig). As highlighted by other studies, some mammals (vervet monkey, Cape and water mongooses, caracal, grysbok and leopard) exhibited an optimum value in their tolerance beyond which habitat may no longer be viable (Suraci et al. 2021). These optimal values are critical to consider when attempting to share the space with wildlife and allow coexistence between mammals and humans in human-dominated landscapes (Oriol-Cotterill et al. 2015). They are also essential when developing connectivity between protected areas (Suraci et al. 2021). Positive associations with human infrastructure may reflect the shield that they provide for some species against predators (e.g. bushbuck) or competitors (e.g. caracal) such as the leopard or an attraction to anthropogenic resources, such as baboon or porcupine (Berger 2007; Hulme-Beaman et al. 2016; Fleming & Bateman 2018).

Species had seasonal variations in their responses. Variables were selected in occupancy models for 11 species in winter (caracal, leopard, blue duiker, grysbok, porcupine, genet, Cape, large grey and water mongooses, bushpig and vervet monkey) and five in summer (leopard, porcupine, genet, Cape grey mongoose and baboon). The significant variables were not the same for all species, nor the direction of the effects, and likely reflected diverse drivers. The seasonal differences could be because of the breeding season, when more individuals would explore new territory, which could explain why fewer variables were important in summer (Kays et al. 2020). The difference observed may reflect relative change in resource availability in the landscape, as well as seasonal change in the intensity of human activities and related disturbances and translated in diverse responses illustrating species-specific trade-offs (Moleón & Sánchez-Zapata 2023). The GRBR is a popular summer holiday destination (Roux et al. 2020), and the seasonal variation in human activities might explain why less species responded to land-uses and disturbance variables in summer. Furthermore, seasonality impacts food availability and resources may be easier to find close to humans in winter than in natural environments, which may explain the attraction for areas with a higher road density in winter for the genet or the bushpig (Hulme-Beaman et al. 2016). Crops, such as maize, would be only available at a certain time of the year in agricultural areas, which may explain why the bushpig used the forest environment less in summer (Moleón & Sánchez-Zapata 2023).

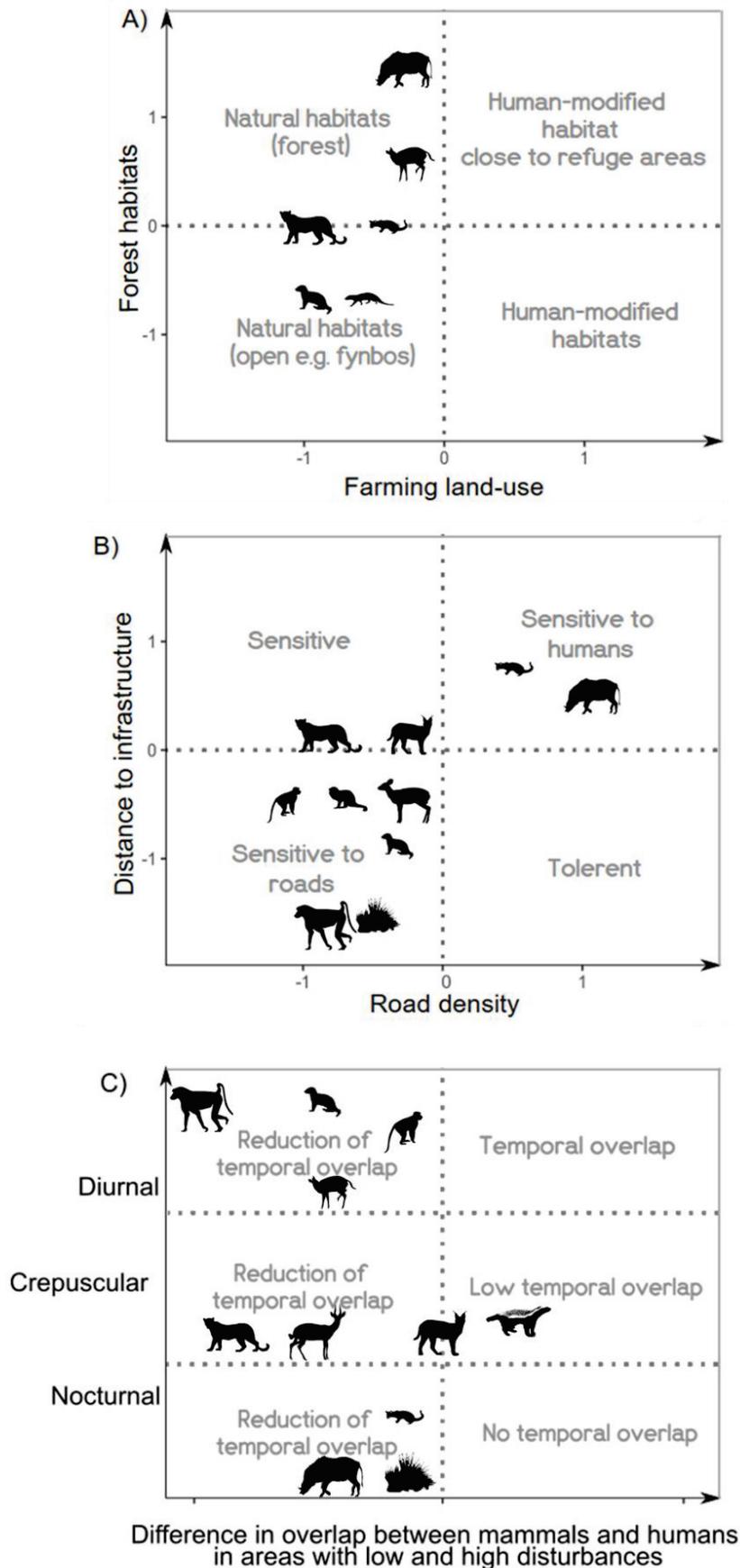
To reduce the risk of the CTs being stolen, we did not set them up on hiking trails or roads, which may have reduced the detection rate of some species, especially for carnivores in the dense forest (Harmsen et al. 2010; Blake & Mosquera 2014). Furthermore, the duration of the study cannot document responses to more gradual changes such as land use, temperature increases, or rare events such as fires, which may also affect habitat use (Moleón & Sánchez-Zapata 2023).

Nine species (baboon, bushbuck, bushpig, blue duiker, genet, leopard, Cape grey mongoose, vervet monkey and porcupine) reduced their overlap with human activities in areas with a high road density and three were detected too rarely in areas with a high density of roads to carry out the analysis (Cape grysbok, water and large grey mongooses), whereas only the Cape grey mongoose showed a shift of activity with the distance to infrastructure. Our results suggested that most species responses to human disturbances may be temporal rather than spatial, as road density affected only six species in the occupancy models, all of which (*i.e.* Cape grysbok, large-spotted genet, bushpig, vervet monkey, Cape grey and water mongoose) responded both in habitat use and niche shift. Furthermore, species expressed a behavioral risk avoidance, by reducing their temporal overlap with human activities, in areas with more road density, where the risk of human encounter are higher as it has been shown in other studies to affect the level of species responses (Frid & Dill 2002; Gavin & Komers 2006). Our results suggested that species were less tolerant to the presence of humans in areas with a high road density, *i.e.* highly frequented by humans. In addition to a change of their temporal niche, some species adjusted their temporal behavior to avoid the direct presence of humans, suggesting their sensitivity to direct human encounters (e.g. bushpig, genet, grysbok and porcupine). A temporal shift of activity reflects a high behavioral flexibility, which all species cannot express (Gaynor et al. 2018). We did not observe a shift from diurnal to nocturnal in the species of the GRBR as shown by other studies (Gaynor et al. 2018; Van Scoyoc et al. 2023). We did not compare the temporal activity at the different seasons, because it would

have reduced the data available for each species. However, previous studies in the KwaZulu-Natal, in South Africa, suggested that there were relatively little seasonal temporal variations for the bushbuck and the blue duiker (Ehlers Smith et al. 2019).

## 4.2 | The concept of anthropodependence

Most of the species seemed to be anthropophilic or synanthropic (Figure 4). Anthropophilic species take advantage of the opportunities to find resources in human modified landscapes while taking advantage of the typical absence of large carnivores in proximity to human areas (Hulme-Beaman et al. 2016; Fleming & Bateman 2018). Because of their tolerance to human disturbances, porcupines, large-spotted genets, baboons, bushpigs and vervet monkeys combined with an attraction for human infrastructure for porcupine and baboon could be good candidates to be classified as anthropophilic. Synanthropic species are categorized by their use of anthropogenic landscapes but without human resources consumption (Hulme-Beaman et al. 2016). They seemed to be either ubiquitous species such as bushbuck, which was detected on 95% of the sites of the area, and was the most common species, or species with large home ranges, able to move in the anthropogenic matrix such as the caracal, honey badger or water mongoose, which had nocturnal or crepuscular behavior, and thus the possibility to avoid human encounters. The Cape grey and large mongooses could also be classified as synanthropic as they did not have a preferred habitat and Cape grey mongoose had a tolerance for human infrastructure. Assessing the contribution of anthropogenic resources in the diet of such a species will help define whether it is synanthropic or anthropodependent in the GRBR context. The blue duiker appeared to be anthropophobic species, preferring natural forest habitats, the most largely habitat protected by the GRNP (Venter et al. 2016b; Ehlers Smith et al. 2018). The grysbok, leopard and large grey mongoose, because of their small number of detections, may rather be considered as anthropophobic species, or occurring at relatively low densities, as they did not occur at high density in the multifunctional landscapes of the GRBR. The low detection of the grysbok may be explained by the fact that it is a fynbos species (Palmer et al. 2016), habitat that was covered by only nine CTs. As we used CTs data, we could not discuss the consumption of food resources and not conclude on two categories from Hulme-Beaman et al. (2016), *i.e.* anthropodependent or anthropophilic species, but some literature on the diet of some species is available. Baboons have been shown to take advantage of the easily accessible food found in bins (Hoffman & O’Riain 2012; Mazue et al. 2023), confirming their anthropophilic behavior. Caracals have been found to predate on domestic cats (Braczkowski et al. 2012), which is a reason for human-wildlife conflict in Cape Town (Nattrass & O’Riain 2020). Caracals and leopards also feed on livestock in some areas (Drouilly et al. 2018), whereas it represents a small proportion of the leopard diet (Martins et al. 2011; Drouilly et al. 2018). This questions the position of the caracal in our classification, which might rather be anthropophilic. The bushbuck benefited from crops (Jansen van Vuuren et al. 2022), water mongooses were generalist species (Do Linh San et al. 2020), as well as genets, suggesting that they might as well be anthropophilic species (Roberts et al. 2007). Research on mammal diet in the GRBR is needed to assess their level of human resources consumption. As suggested by other researchers, it would be valuable to combine CT data and diet analyses (Van Scoyoc et al. 2023).



**FIGURE 4** Summary of the results adapted from Hulme-Beaman et al. (2016) A) Spatial overlap with human habitats. B) Effect of human disturbance on the tolerance of species adapted from Sévêque et al. (2020). Humans correspond to top-down disturbances, whereas structural disturbances correspond to bottom-up disturbances. C) expected temporal activity in responses to high and low density of roads.

### 4.3 | Conservation implications

Given the diversity of species responses to humans in the GRBR, landscape management approaches that consider the ecological needs of several species will be more appropriate, as also recommended by other researchers (Zungu et al. 2020). Adding human disturbances and mammal temporal activity dimensions to Hulme-Beaman et al. (2016) framework appear to be important in refining our understanding of mammals use of anthropogenic landscapes (Figure 4). This completed framework could serve as a baseline to understand the processes facilitating coexistence (Carter & Linnell 2023). For anthropophobic species, such as the blue duiker, conservation action must be taken, e.g. protection of natural habitats. It will also benefit anthropophilic and synanthropic species, which use these areas as refuges or to move within the anthropogenic matrices. For synanthropic species, connectivity is the essence in such patchy multifunctional landscapes, especially if they have a specialized diet. Vast networks of corridors with natural vegetation and low disturbance by humans need to be properly implemented so that mammals can move through the landscapes. The existence of CBAs in the GRBR is a move in the right direction, provided that the fencing of properties is restricted as much as building (CapeNature 2017). To be efficient, conservation management plans need to be cautious about anthropophilic species, such as baboons, because of their attraction to human food resources. They can represent a sporadic nuisance for humans, and both baboons and humans can negatively impact each other, which will prevent coexistence (Carter & Linnell 2023). Studying human impacts on wildlife is key to work on coexistence in anthropogenic landscapes (Suraci et al. 2021), but studying human adaptation to wildlife is also required, as they must adapt to the constraints of wildlife (Carter & Linnell 2023). Land use and urban planning must work on interfaces between protected areas and anthropogenic matrices, as these may exacerbate tensions (Blanco et al. 2020). Conservationists should be realistic about the impact of conservation measures and, when appropriate openly discuss it with the public to co-develop sustainable solutions (McShane et al. 2011). More natural habitat patches should be integrated into human landscapes, under private and municipal initiatives, to provide connectivity for species movement and refugia (Ehlers Smith et al. 2018; Brennan et al. 2022). These measures would not only benefit wildlife, but could also contribute to people's quality of life and wellbeing (Obura et al. 2021).

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### References

Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., Beard, K.H. & Pearse, W.D. (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, 6, eabb8458.

- Baard, J., Durrheim, G., Hanekom, N., Hayes, J.S., Kraaij, T., Kruger, N., Ngubeni, N., Randall, R.M., Russell, I.A., Seydack, A.H.W., Smith, K., Van der Vyer, L. & Vermeulen, W.J. (2015). Garden Route National Park - State of knowledge.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.*, 3, 620–623.
- Blake, J.G. & Mosquera, D. (2014). Camera trapping on and off trails in lowland forest of Eastern Ecuador: does location matter?, 11.
- Blanco, J., Bellón, B., Fabricius, C., O. Roque, F., Pays, O., Laurent, F., Fritz, H. & Renaud, P. (2020). Interface processes between protected and unprotected areas: A global review and ways forward. *Glob Change Biol*, 26, 1138–1154.
- Braczkowski, A., Watson, L., Coulson, D., Lucas, J., Peiser, B. & Rossi, M. (2012). The Diet of Caracal, (*Caracal caracal*), in Two Areas of the Southern Cape, South Africa as Determined by Scat Analysis. *South African Journal of Wildlife Research*, 42, 111–116.
- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N. & Kremen, C. (2022). Functional connectivity of the world's protected areas. *Science*, 376, 1101–1104.
- CapeNature. (2017). Western Cape Biodiversity Spatial Plan Handbook.
- Carter, N.H. & Linnell, J.D.C. (2023). Building a resilient coexistence with wildlife in a more crowded world. *PNAS Nexus*, 2, pgad030.
- Cazalis, V., Princé, K., Mihoub, J.-B., Kelly, J., Butchart, S.H.M. & Rodrigues, A.S.L. (2020). Effectiveness of protected areas in conserving tropical forest birds. *bioRxiv*, 2020.01.21.912345.
- Conn, P.B., Johnson, D.S., Williams, P.J., Melin, S.R. & Hooten, M.B. (2018). A guide to Bayesian model checking for ecologists. *Ecol Monogr*, 88, 526–542.
- Crisp, A.G. (2015). Development role players' knowledge of ecological infrastructure in Eden district, South Africa.
- Cumming, G.S., Allen, C.R., Ban, N.C., Biggs, D., Biggs, H.C., Cumming, D.H.M., De Vos, A., Epstein, G., Etienne, M., Maciejewski, K., Mathevet, R., Moore, C., Nenadovic, M. & Schoon, M. (2015). Understanding protected area resilience: a multi-scale, social-ecological approach. *Ecological Applications*, 25, 299–319.
- Department of Forestry, Fisheries and the Environment. (2020). South African National Landcover Data.
- Diaz, S. (2019). Pervasive human-driven decline of life on Earth points to the need for profound change. *Science*, 331, 341–346.
- digikam team. (2001). DigiKam [Computer software].
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.
- Do Linh San, E., Nqinana, A., Madikiza, Z.J. & Somers, M.J. (2020). Diet of the marsh mongoose around a non-permanent reservoir: response of a generalist opportunist forager to the absence of crabs. *African Zoology*, 55, 240–244.
- Drouilly, M., Nattrass, N. & O'Riain, M.J. (2018). Dietary niche relationships among predators on farmland and a protected area: Diet of Predators on Contrasting Land Uses. *Jour. Wild. Mgmt.*, 82, 507–518.
- Ehlers Smith, Y.C., Ehlers Smith, D.A., Ramesh, T. & Downs, C.T. (2018). Forest habitats in a mixed urban-agriculture mosaic landscape: patterns of mammal occupancy. *Landscape Ecol*, 33, 59–76.

- Ehlers Smith, Y.C., Ehlers Smith, D.A., Ramesh, T. & Downs, C.T. (2019). Novel predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species. *Behavioural Processes*, 159, 9–22.
- Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, 19, 589–606.
- Fischer, J. & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265–280.
- Fleming, P.A. & Bateman, P.W. (2018). Novel predation opportunities in anthropogenic landscapes. *Animal Behaviour*, 138, 145–155.
- Frid, A. & Dill, L.M. (2002). Human-caused Disturbance Stimuli as a Form of Predation Risk. *CE*, 6, art11.
- Gatiso, T.T., Kulik, L., Bachmann, M., Bonn, A., Bösch, L., Eirdosh, D., Freytag, A., Hanisch, S., Heurich, M., Sop, T., Wesche, K., Winter, M. & Kühn, H.S. (2022). Effectiveness of protected areas influenced by socio-economic context. *Nat Sustain*, 861–868.
- Gavin, S.D. & Komers, P.E. (2006). Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? *Can. J. Zool.*, 84, 1775–1780.
- Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.
- Gelman, A. (2006). Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal.*, 1.
- Gelman, A., Jakulin, A., Pittau, M.G. & Su, Y.-S. (2008). A weakly informative default prior distribution for logistic and other regression models. *Ann. Appl. Stat.*, 2.
- Harmsen, B.J., Foster, R.J., Silver, S., Ostro, L. & Doncaster, C.P. (2010). Differential Use of Trails by Forest Mammals and the Implications for Camera-Trap Studies: A Case Study from Belize: Trail Use by Neotropical Forest Mammals. *Biotropica*, 42, 126–133.
- Hoffman, T.S. & O’Riain, M.J. (2012). Landscape requirements of a primate population in a human-dominated environment. *Front Zool*, 9, 1.
- Hulme-Beaman, A., Dobney, K., Cucchi, T. & Searle, J.B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, 31, 633–645.
- Jansen van Vuuren, A., Fritz, H. & Venter, J.A. (2022). Five small antelope species diets indicate different levels of anthrodependence in the Overberg Renosterveld, South Africa. *African Journal of Ecology*, n/a.
- Karant, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R. & Kumar, N.S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proc. R. Soc. B.*, 284, 20161860.
- Kays, R., Arbogast, B.S., Baker-Whetton, M., Beirne, C., Boone, H.M., Bowler, M., Burneo, S.F., Cove, M.V., Ding, P., Espinosa, S., Gonçalves, A.L.S., Hansen, C.P., Jansen, P.A., Kolowski, J.M., Knowles, T.W., Lima, M.G.M., Millspaugh, J., McShea, W.J., Pacifici, K., Parsons, A.W., Pease, B.S., Rovero, F., Santos, F., Schuttler, S.G., Sheil, D., Si, X., Snider, M. & Spironello, W.R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, 11, 700–713.
- Kéry, M. & Schaub, M. (2012). Estimation of Occupancy and Species Distributions from Detection/Nondetection Data in Metapopulation Designs Using Site-Occupancy Models. In: *Bayesian Population Analysis using WinBUGS*. Elsevier, pp. 413–461.

- Leighton, G.R.M., Bishop, J.M., Merondun, J., Winterton, D.J., O’Riain, M.J. & Serieys, L.E.K. (2022). Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. *Animal Conservation*, 25, 244–258.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2017). *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier.
- Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. (2011). Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis: Leopard diet determination by GPS and scat analysis. *Journal of Zoology*, 283, 81–87.
- Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S.L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O. & Watson, J.E.M. (2020). Area-based conservation in the twenty-first century. *Nature*, 586, 217–227.
- Mazue, F., Guerbois, C., Fritz, H., Rebut, N. & Petit, O. (2023). Less bins, less baboons: reducing access to anthropogenic food effectively decreases the urban foraging behavior of a troop of chacma baboons (*Papio hamadryas ursinus*) in a peri-urban area. *Primates*, 64, 91–103.
- McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A., Monteferri, B., Mutekanga, D., Thang, H.V., Dammert, J.L., Pulgar-Vidal, M., Welch-Devine, M., Peter Brosius, J., Coppolillo, P. & O’Connor, S. (2011). Hard choices: Making trade-offs between biodiversity conservation and human well-being. *Biological Conservation*, 144, 966–972.
- Moleón, M. & Sánchez-Zapata, J.A. (2023). Extending the dynamic landscape of fear in a human-dominated world. *Trends in Ecology & Evolution*, 38, 215–216.
- Natrass, N. & O’Riain, M.J. (2020). Contested natures: conflict over caracals and cats in Cape Town, South Africa. *Journal of Urban Ecology*, 6, juaa019.
- Nickel, B.A., Suraci, J.P., Allen, M.L. & Wilmers, C.C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, 241, 108383.
- Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods Ecol Evol*, 7, 1457–1462.
- Obura, D.O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoilys, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M. & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, 373, 746–748.
- O’Connell, A.F., Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R. & Gilbert, A.T. (2006). Estimating Site Occupancy and Detection Probability Parameters for Meso- And Large Mammals in a Coastal Ecosystem. *The Journal of Wildlife Management*, 70, 1625–1633.
- Ordeñana, M.A., Crooks, K.R., Boydston, E.E., Fisher, R.N., Lyren, L.M., Siudyla, S., Haas, C.D., Harris, S., Hathaway, S.A., Turschak, G.M., Miles, A.K. & Van Vuren, D.H. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy*, 91, 1322–1331.
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015). Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 124, 1263–1273.
- Osner, N. (2022). TrapTagger [Computer software].

- Palmer, G., Birss, C., Kerley, G.I.H., Feely, J., Peinke, D. & Castley, G. (2016). A conservation assessment of *Raphicerus melanotis*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa, 7.
- Pardo, L.E., Bombaci, S.P., Huebner, S., Somers, M.J., Fritz, H., Downs, C., Guthmann, A., Hetem, R.S., Keith, M., le Roux, A., Mgqatsa, N., Packer, C., Palmer, M.S., Parker, D.M., Peel, M., Slotow, R., Strauss, W.M., Swanepoel, L., Tambling, C., Tsie, N., Vermeulen, M., Willi, M., Jachowski, D.S. & Venter, J.A. (2021). Snapshot Safari: a large-scale collaborative to monitor Africa's remarkable biodiversity. *S. Afr. J. Sci.*, 117.
- Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10, 439–446.
- Peral, C., Landman, M. & Kerley, G.I.H. (2022). The inappropriate use of time-to-independence biases estimates of activity patterns of free-ranging mammals derived from camera traps. *Ecology and Evolution*, 12, e9408.
- Plummer. (2022). rjags: Bayesian Graphical Models using MCMC. R package version 4-13.
- QGIS Association. (2022). QGIS Geographic Information System.
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *JABES*, 14, 322–337.
- Riley, S.P.D. (2006). Spatial Ecology of Bobcats and Gray Foxes in Urban and Rural Zones of a National Park. *The Journal of Wildlife Management*, 70, 1425–1435.
- Roberts, P.D., Somers, M.J., White, R.M. & Nel, J.A.J. (2007). Diet of the South African large-spotted genet *Genetta tigrina* (Carnivora, Viverridae) in a coastal dune forest. *Acta Theriol*, 52, 45–53.
- Rosenzweig, M.L. (2003). Reconciliation ecology and the future of species diversity. *Oryx*, 37, 194–205.
- Roux, Dirk J., M. Kyle S. Smith, Izak P. J. Smit, Stefanie Freitag, Liandi Slabbert, Mohlamatsane M. Mokhatla, Jessica Hayes, et Nelsiwe P. Mpapane. (2020) Cultural Ecosystem Services as Complex Outcomes of People–Nature Interactions in Protected Areas. *Ecosystem Services* 43. <https://doi.org/10.1016/j.ecoser.2020.101111>.
- SANParks. (2020). Garden Route National Park: Park Management Plan For the period 2020 - 2029. Pretoria: Department of Environment, Forestry and Fisheries.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.
- Scholte, P., Pays, O., Adam, S., Chardonnet, B., Fritz, H., Mamang, J., Prins, H.H.T., Renaud, P., Tadjó, P. & Moritz, M. (2021). Conservation overstretch and long-term decline of wildlife and tourism in the Central African savannas. *Conservation Biology*, *cobi.13860*.
- Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W. & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95, 1689–1705.
- Shumba, T., De Vos, A., Biggs, R., Esler, K.J., Ament, J.M. & Clements, H.S. (2020). Effectiveness of private land conservation areas in maintaining natural land cover and biodiversity intactness. *Global Ecology and Conservation*, 22, e00935.
- Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forrester, T., Green, A.M., Haight, J., Harris, N.C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P.E., Lewis, J.S., McInturff, A., McShea, W.,

- Murphy, T.W., Palmer, M.S., Parsons, A., Parsons, M.A., Pendergast, M.E., Pekins, C., Prugh, L.R., Sager-Fradkin, K.A., Schuttler, S., Şekercioğlu, Ç.H., Shepherd, B., Whipple, L., Whittington, J., Wittemyer, G. & Wilmers, C.C. (2021). Disturbance type and species life history predict mammal responses to humans. *Glob Change Biol*, 27, 3718–3731.
- Taylor, W.A., Child, M.F., Lindsey, P.A., Nicholson, S.K., Relton, C. & Davies-Mostert, H.T. (2021). South Africa's private wildlife ranches protect globally significant populations of wild ungulates. *Biodivers Conserv*, 30, 4111–4135.
- UNEP-WCMC, IUCN & NGS. (2020). Protected Planet Report 2020. Cambridge UK; Gland, Switzerland; and Washington, D.C., USA.
- Van Scoyoc, A., Smith, J.A., Gaynor, K.M., Barker, K. & Brashares, J.S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, 1365–2656.13892.
- Venter, J., Ehlers Smith, Y. & Seydack, A. (2016a). A conservation assessment of *Potamochoerus larvatus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 5.
- Venter, J., Seydack, A., Ehlers Smith, Y., Uys, R. & Child, M.F. (2016b). A conservation assessment of *Philantomba monticola*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 9.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016c). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun*, 7, 12558.
- Western Cape Government. (2019). Socio-economic profile: Garden Route District Municipality.
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.
- Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V. & Williams, T. (2013). Scale Dependent Behavioral Responses to Human Development by a Large Predator, the Puma. *PLoS ONE*, 8, e60590.
- Woodgate, Z., Drouilly, M., Distiller, G. & O'Riain, M.J. (2023). The Effect of Multi-Use Landscapes on Mammal Assemblages and Its Implication for Conservation. *Land*, 12, 599.
- Yirga, G., De longh, H.H., Leirs, H., Gebrihiwot, K., Deckers, J. & Bauer, H. (2012). Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia: Adaptability of large carnivores to changing anthropogenic food sources. *Journal of Animal Ecology*, 81, 1052–1055.
- Zungu, M.M., Maseko, M.S.T., Kalle, R., Ramesh, T. & Downs, C.T. (2020). Factors affecting the occupancy of forest mammals in an urban-forest mosaic in EThekweni Municipality, Durban, South Africa. *Urban Forestry & Urban Greening*, 48, 126562.

## Supplementary material for the manuscript 2: Spatio-temporal overlap between African mammals and humans in a multifunctional landscape: insights on the concept of anthropodependence

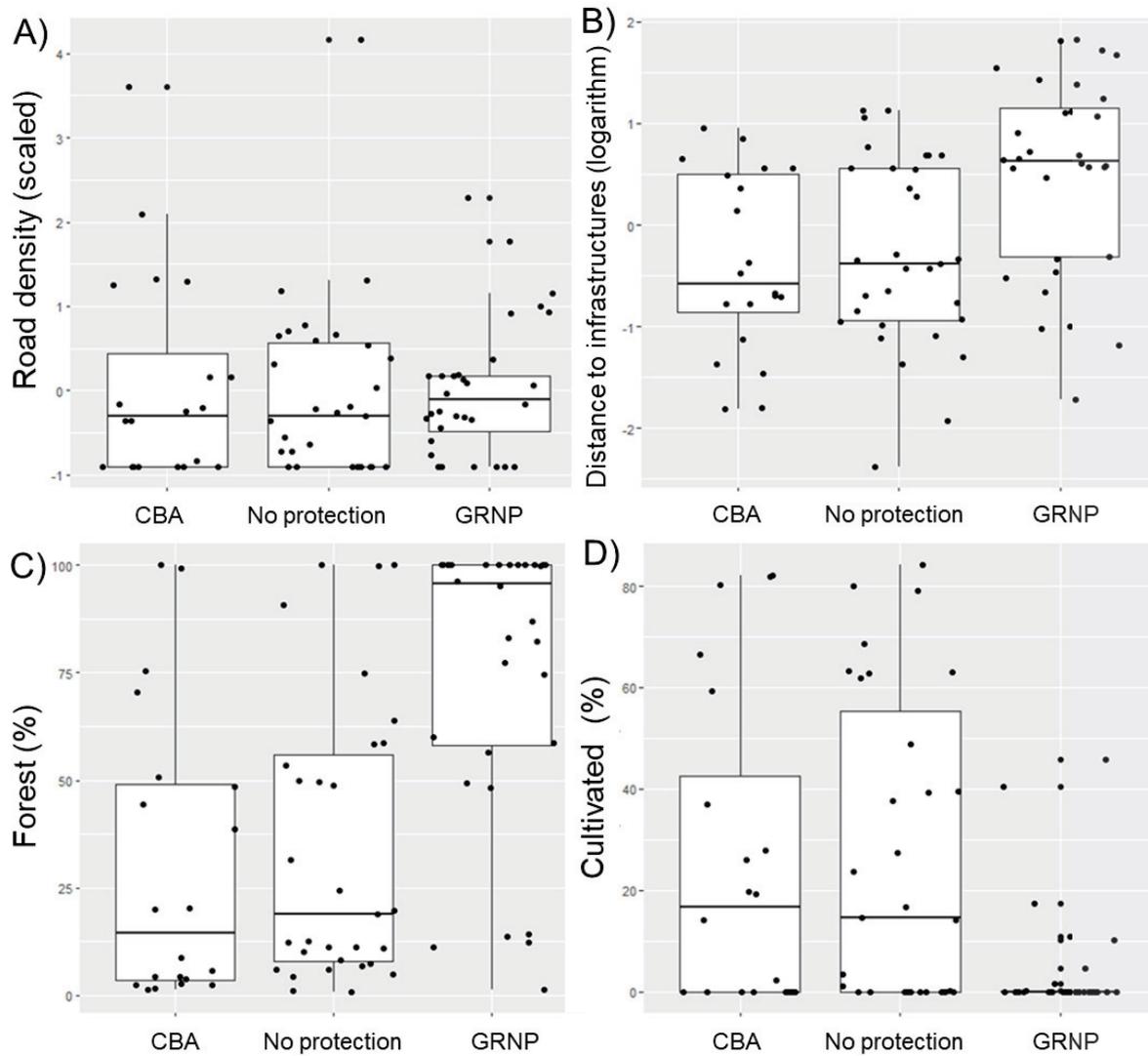
### Supplementary methods

**Data collection.** We set-up 30 cameras in the Garden Route National Park, 18 in CBAs and 26 in human-dominated areas, without any protection status. We used shapefiles furnished by SANParks for the GRNP borders and from CapeNature for CBAs, to attribute a conservation protection status for each cameras.

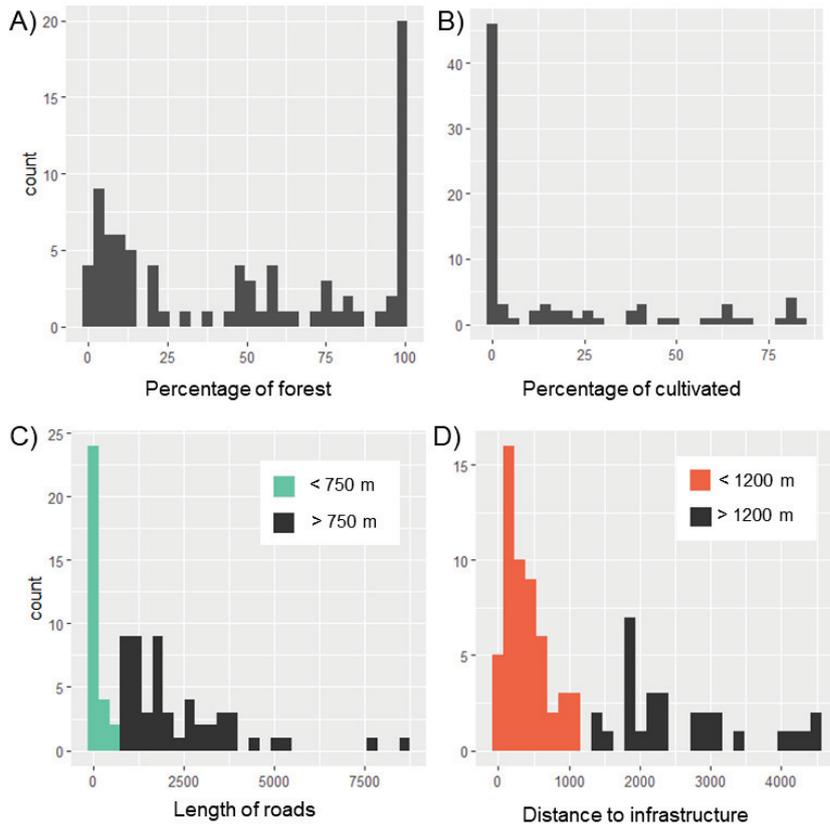
**Occupancy analyses.** We performed a single species, single-season, occupancy modelling (MacKenzie et al. 2017), using the R package 'unmarked' and the 'occu' function, and independently ran a model for summer and winter, with 3 months each (Fiske & Chandler 2021). For each site, we measured the visibility in front of the camera and the height of the camera as it might have influence detection. We also noted if the camera was set-up on a trail or not, in order to correct for detection bias. For each species, we ran a model with the protection status of the camera site as the only variable for occupancy and we extracted the predicted values. We tested the goodness of fit, and only represented models with a p-value > 5%. The models for both seasons for the vervet monkey, genet and baboon and during winter for the caracal and bushpig, had p-value < 5% showing enough in the goodness of fit test and were not represented because of lack of fit. We plotted the predicted occupancy value per species for each protection status (Figure S4).

**Temporal analyses.** To study the temporal niche of mammals we calculated their temporal activity patterns in the Garden Route National Park (GRNP), Critical Biodiversity Areas (CBAs) and areas without protection status (Ridout & Linkie 2009). To see whether they were using the same temporal niche as humans, we calculated the temporal activity of each species and the overlap with human. Humans regrouped detection of humans, vehicles and bicycles. We calculated the  $\Delta 4$  overlap coefficient ('overlapEst' function, 'overlap' package), which represents the proportion of overlap between the two activities curves, with zero meaning that there is no overlap and 1 that the two curves overlap completely (Ridout & Linkie 2009). To compare the observed value with the distribution of the null hypothesis, we randomly simulated 1000 temporal activity curves for each mammal ("resample function", "overlap" package) to estimate the 95% confidence interval for each overlap value (Karanth et al. 2017). Species considered for the analyses had at least 20 observations (Figure S6). As recommended by Peral et al. (2022), we did not filter the data for independence.

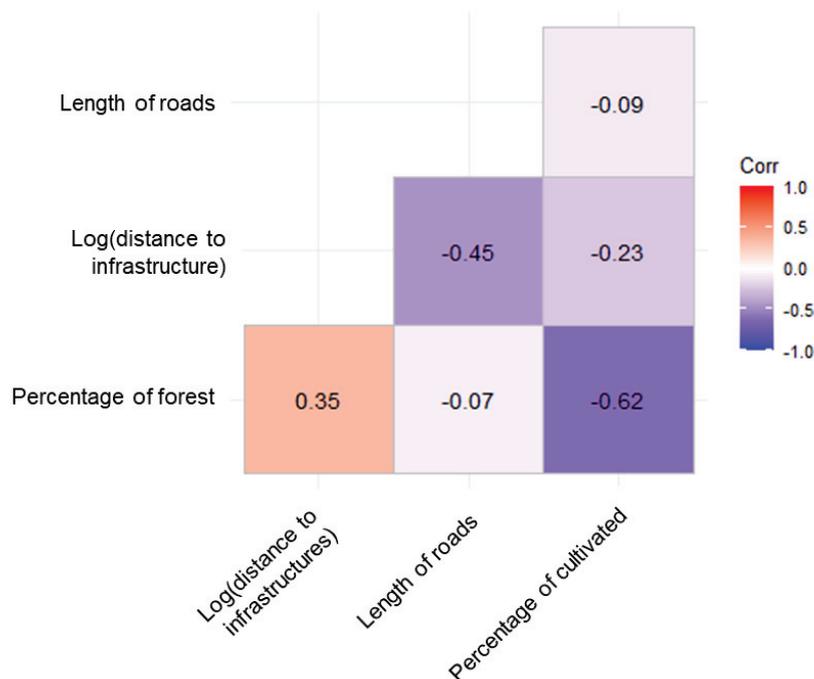
## Figures



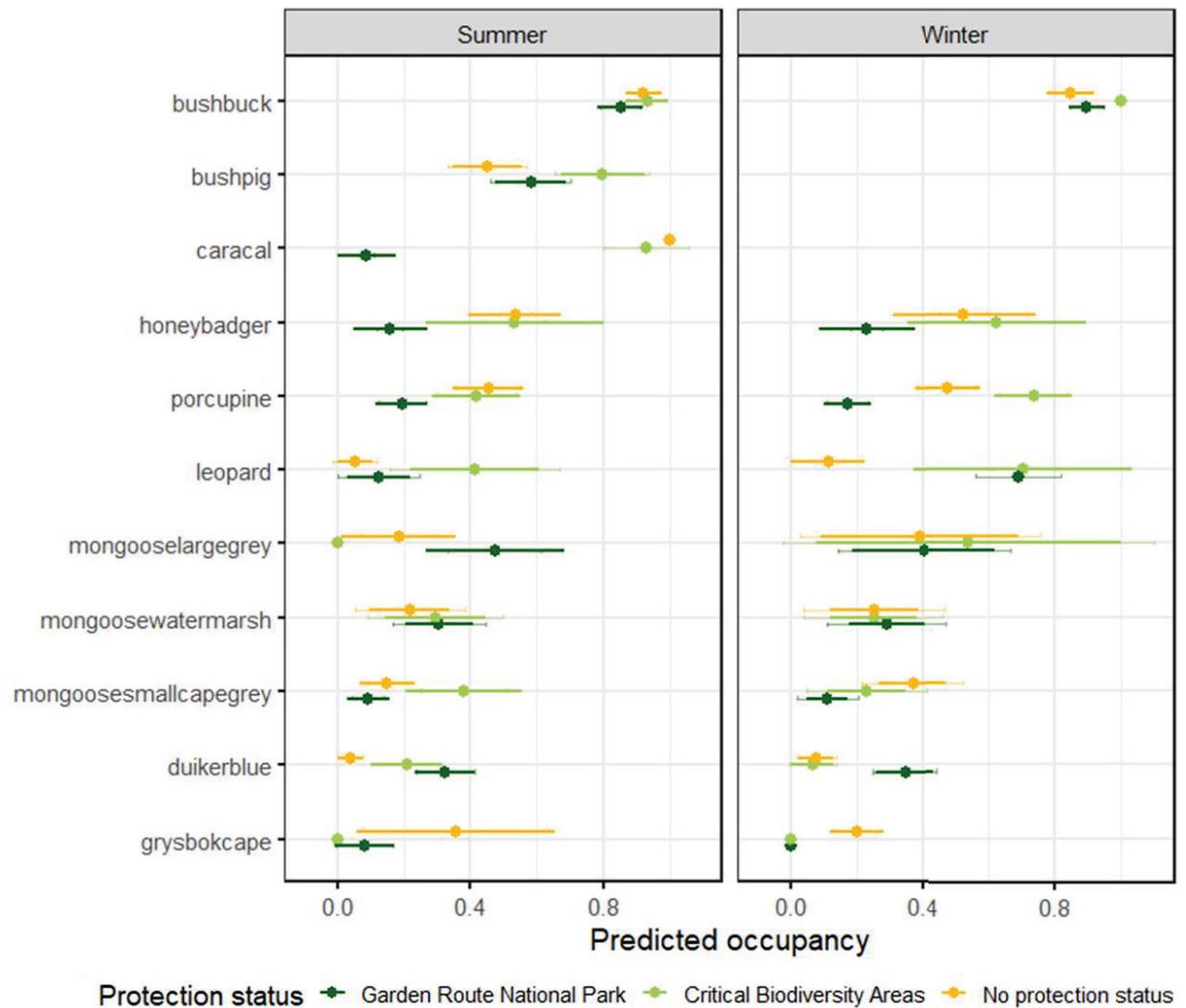
**FIGURE S1** Description of the different type of status of protection using the variables used in the occupancy modelling



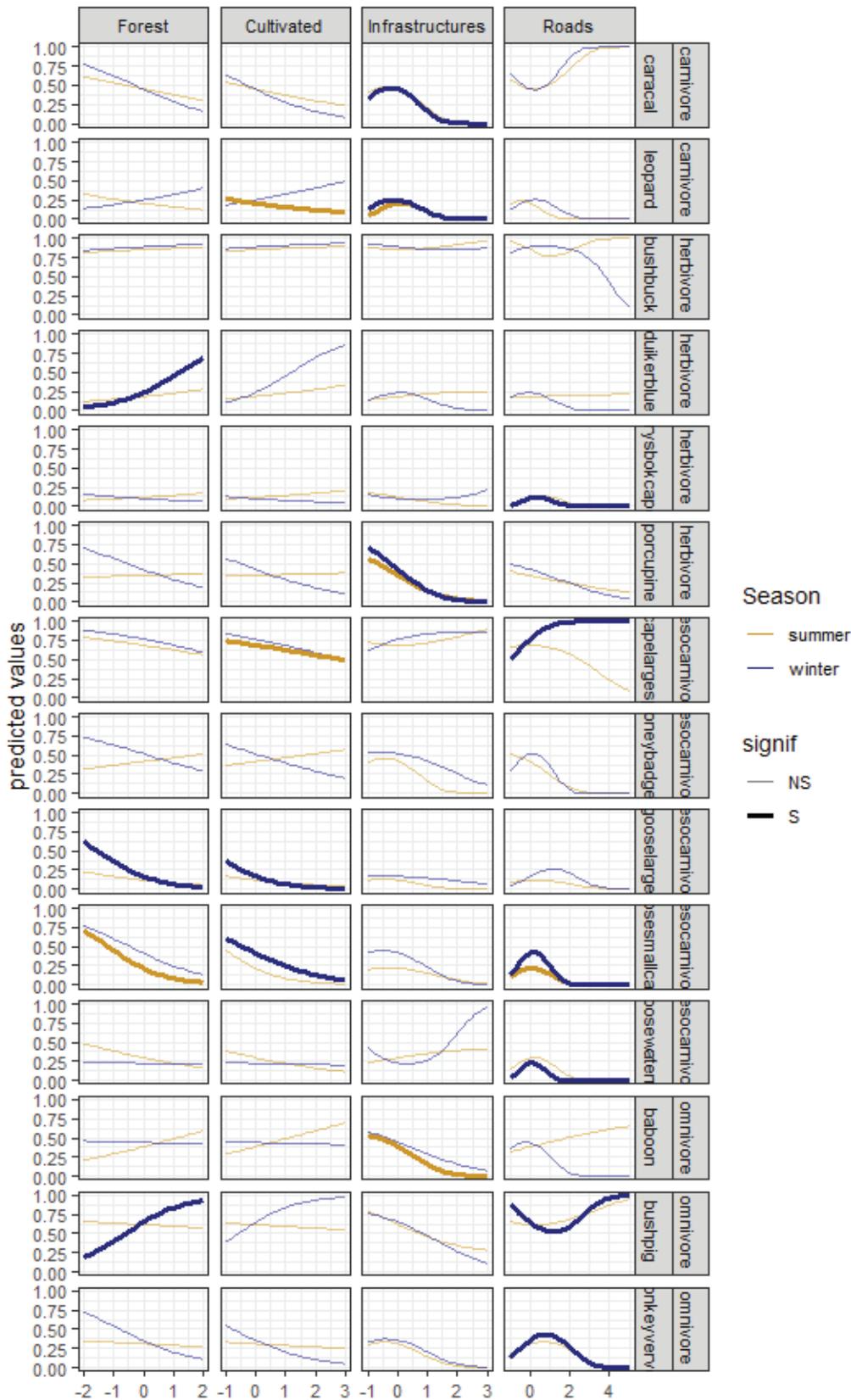
**FIGURE S2** Variables used for the occupancy models. A) percentage of forest, B) percentage of cultivated areas, C) length of roads (green bars represent a length < 750 m), D) distance to infrastructure (coral bars represent a distance < 1200 m).



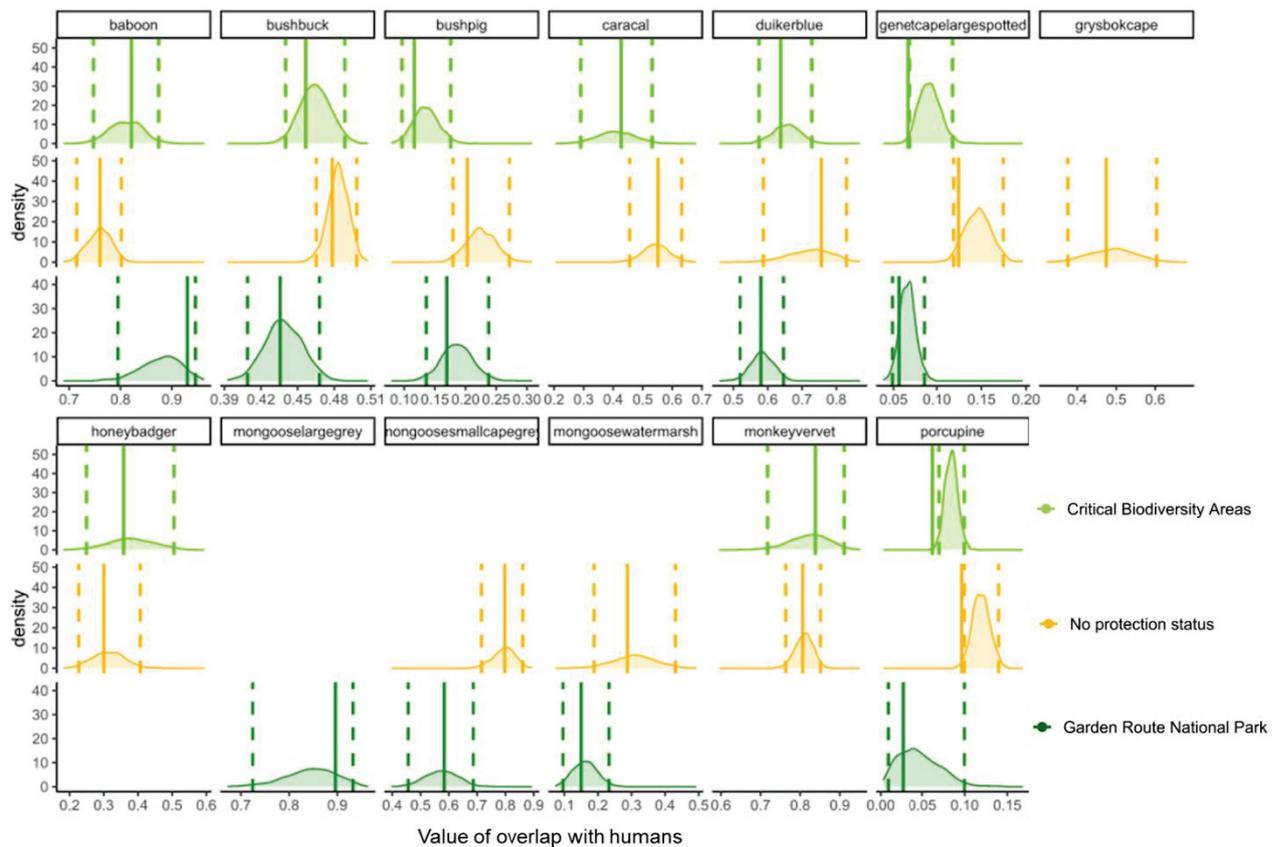
**FIGURE S3** Absence of correlation between the variables used in the occupancy models.



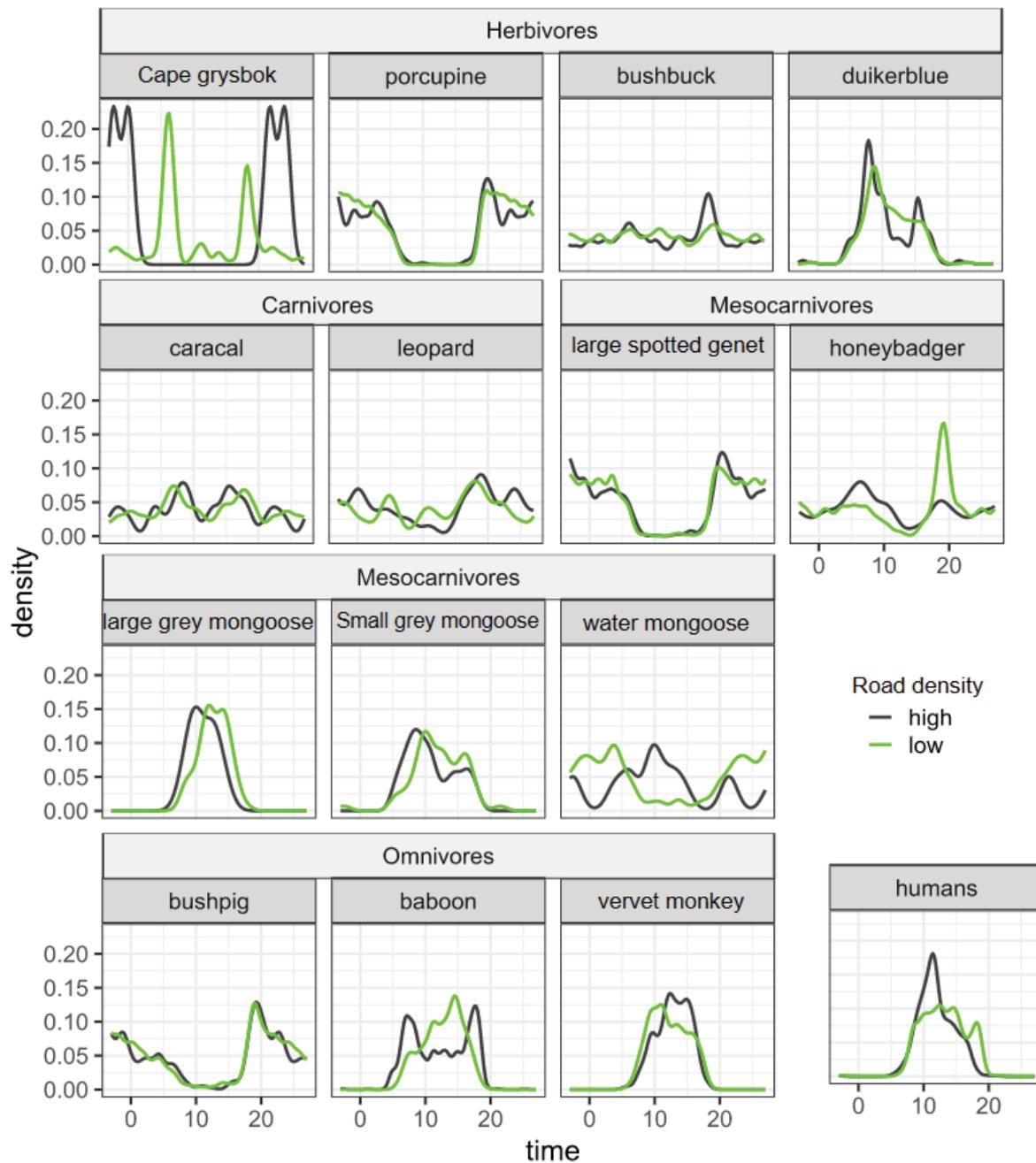
**FIGURE S4** Predicted occupancy probability of selected species between the three types of protection status. The lines represent the SE (dark) and inflated SE (light). The models for both seasons for the vervet monkey, genet and baboon and during winter for caracal and bushpig, had  $p$ -value < 5% in the goodness of fit test and were not represented because of lack of fit. Different patterns emerged regarding the importance of site protection status on the occupancy of species: some were more likely to occupy wild areas (blue duiker, leopard), other prefer CBAs (porcupine, bushpig), had no preference (bushbuck, water mongoose) or preferably occupy human-dominated areas (caracal, honey badger). The latter similarly occupied areas with no status and CBAs, suggesting that they rely on CBAs to persist in human-dominated areas. The lower variation in occupancy between the three types of protection status, suggest there might exist other variables explaining species occupancy in the Garden Route Biosphere Reserve.



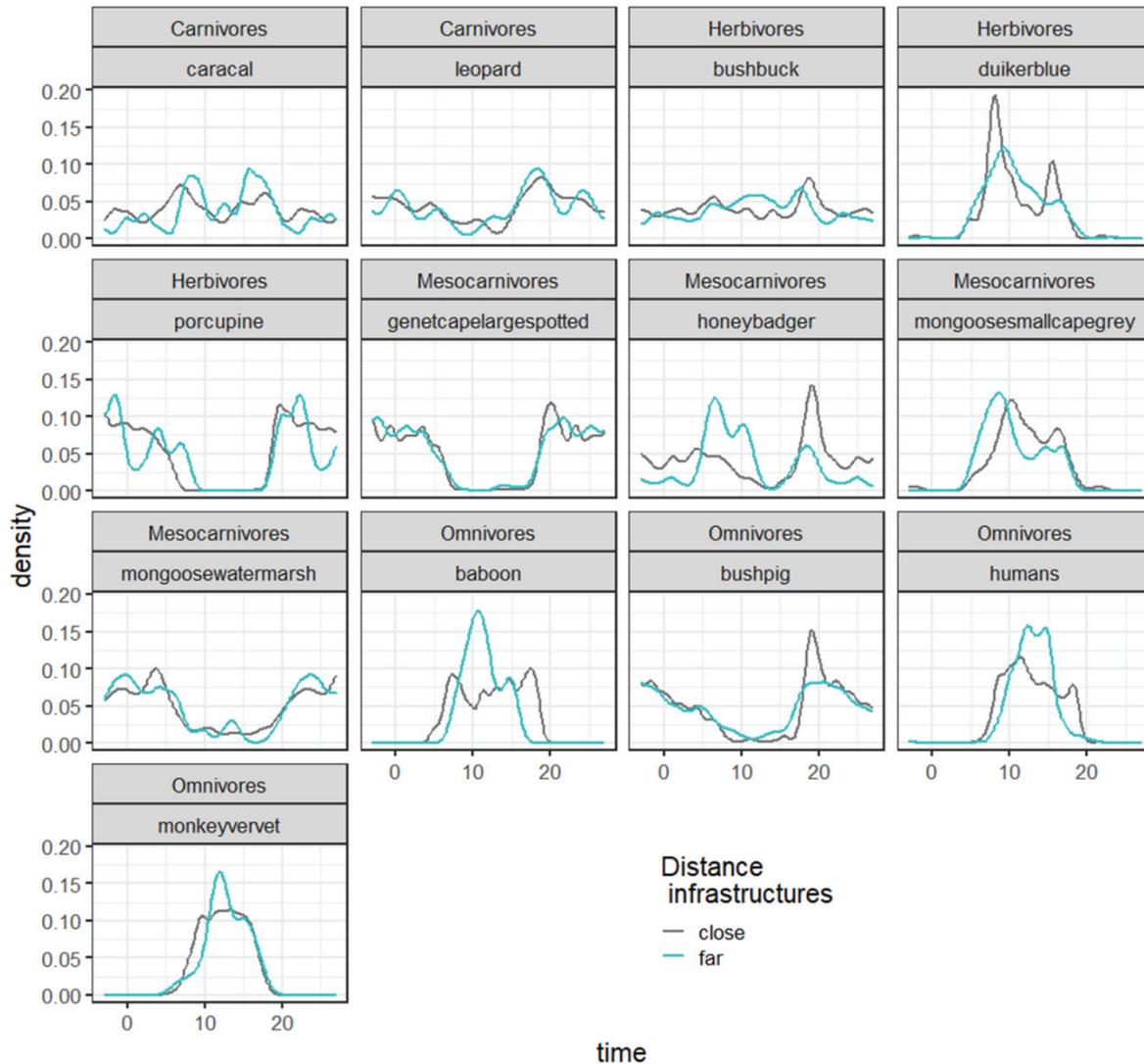
**FIGURE S5** Predicted values for the different variables tested for 14 species of the Garden Route, sorted by diet. The predicted are represented for the two seasons: winter is represented by blue triangles and summer in light brown circles.



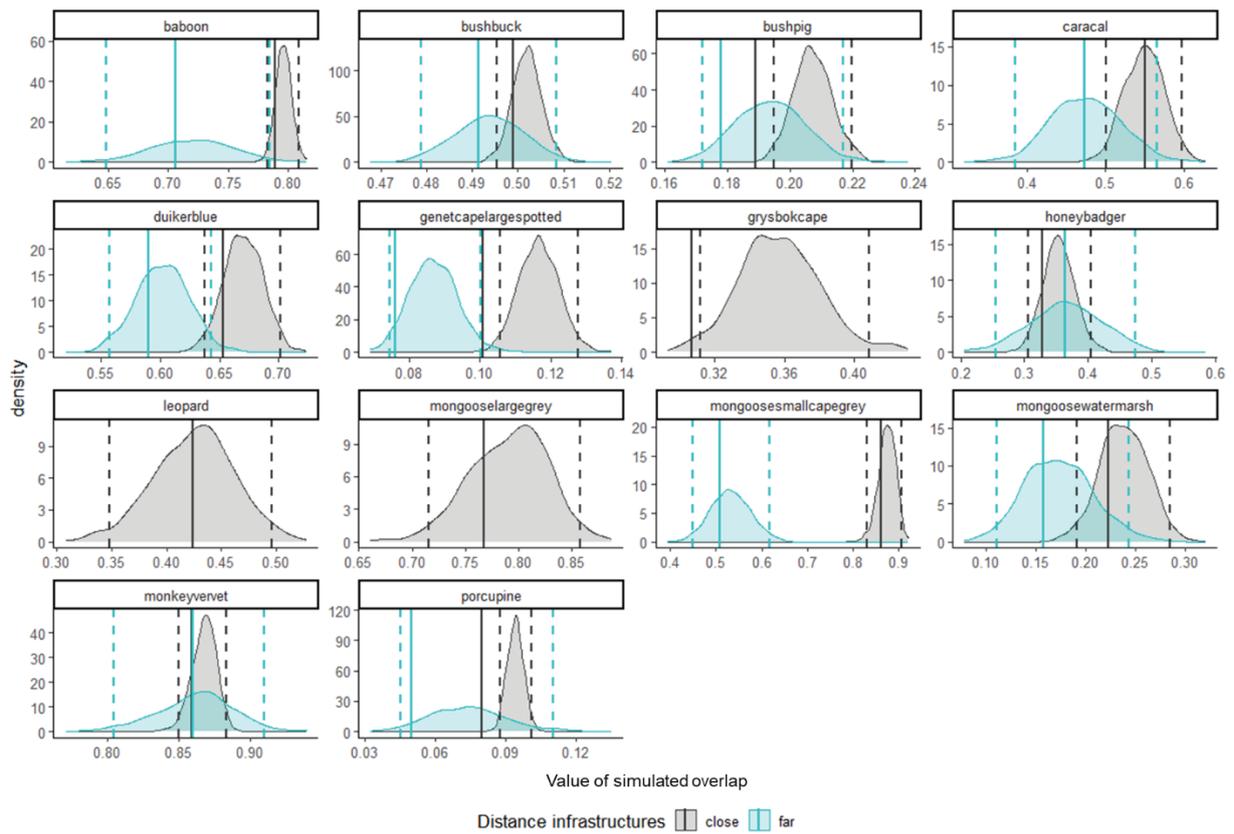
**FIGURE S6** Overlap between mammals and human activity per protection type (CBAs in light green, AWPS in yellow and the GRNP in green). The solid lines represent the observed overlap between the different mammals and human temporal activity. The dotted lines represent the 95% credible interval of the randomly generated overlap. For all species, the observed overlap between species and human, in each protection status areas, was within the confidence interval of the distributions generated using the random records except for porcupine in CBA and areas without protection status, genet in CBA, showing their temporal behavior adjustment to direct presence of humans. The expected overlap with humans: was higher in CBAs, than it was in areas with no protection status and it was higher than in the GRNP for the bushbuck ; was lower in GRNP than in the two other areas for the blue duiker ; was higher in areas with no protection status than it was in the GRNP and in CBAs for the porcupine and for the genet ; higher in areas with no protection status than it was in the GRNP for the Cape grey mongoose and the water mongoose ; was higher in the GRNP than in CBAs and than it was in areas with no protection status for baboon ; was higher in areas with no protection status than it was in the GRNP, and lower in CBAs for the bushpig. The differences noticed in the GRNP for the baboon and the bushbuck temporal responses might be explained by the fact that baboons may be persecuted outside of protected areas so they reduce their overlap with humans, whereas, the likelihood for the bushbuck to be poached outside of the GRNP might be lower, explaining their higher overlap with humans.



**FIGURE S7** Temporal activity of the species of the Garden Route and humans (humans, cyclists, vehicles), sorted by diet and colored by the level of density of roads. Temporal activity in areas with high road density are represented in grey and with low road density in green. All the data collected during the camera trap survey were used. Only species with more than 20 observations were represented. The density were calculated using the 'densityPlot' function from 'overlap' R package.



**FIGURE S8** Temporal activity of the species of the Garden Route and humans (humans, cyclists, vehicles), sorted by diet and colored by their distance to infrastructure. All the data collected during the camera trap survey were used. Temporal activity in areas close to human infrastructure are represented in grey and far from human infrastructure in blue. Only species with more than 20 observations were represented. The density were calculated using the 'densityPlot' function from 'overlap' R package.



**FIGURE S9** Simulated overlap value of a species between areas close and far from human infrastructure. The dotted lines represent the 95% credible interval. The solid line represents the true value of occupancy. Overlap with human in areas close to human infrastructure are represented in grey and far from human infrastructure in blue.

## Tables

**TABLE S1** Table of the number of presence in the detection matrix (grouped by 7 days) during the two seasons on the 75 sites per species.

Common name	Scientific name	Order	Number of detections in winter	Number of detections in summer
Bushbuck	<i>Tragelaphus scriptus</i>	Artiodactyla	570	501
South African large-spotted genet	<i>Genetta tigrina</i>	Carnivora	225	213
Cape porcupine	<i>Hystrix africaeaustralis</i>	Rodentia	169	101
Bushpig	<i>Potamochoerus larvatus</i>	Artiodactyla	154	102
Chacma baboon	<i>Papio ursinus ursinus</i>	Primates	88	115
Blue duiker	<i>Philantomba monticola</i>	Artiodactyla	63	81
Vervet monkey	<i>Cercopithecus pygerythrus</i>	Primates	52	57
Cape grey mongoose	<i>Herpestes pulverulentus</i>	Carnivora	48	18
Caracal	<i>Caracal caracal</i>	Carnivora	48	24
Water mongoose	<i>Atilax paludinosus</i>	Carnivora	32	37
Honey badger	<i>Mellivora capensis</i>	Carnivora	22	36
Cape Gysbok	<i>Raphicerus melanotis</i>	Artiodactyla	13	18
Large grey mongoose	<i>Herpestes ichneumon</i>	Carnivora	13	18
Leopard	<i>Panthera pardus</i>	Carnivora	12	17
Humans	<i>Homo sapiens</i>	Primates	246	166

**TABLE S2** Outputs of the occupancy modelling, classed by diet group.

<b>Carnivores</b>						
<b>Species</b>	<b>Season</b>	<b>Variables</b>	<b>Estimate</b>	<b>2.5 % CI</b>	<b>97.5 % CI</b>	<b>Rhat</b>
<b>Caracal</b>	<b>Summer</b>	Cultivated	0.30	-0.68	1.46	1.000
		Forest	-0.32	-1.46	0.69	1.000
		Infrastructures	-0.54	-1.58	0.47	1.001
		Infrastructures <sup>2</sup>	-0.72	-1.68	0.45	1.003
		Roads	-0.13	-1.27	1.12	1.002
		Roads <sup>2</sup>	0.35	-0.23	1.44	1.002
	<b>Winter</b>	Cultivated	-0.48	-1.48	0.44	1.001
		Forest	-0.71	-1.76	0.24	1.001
		Infrastructures	-0.54	-1.46	0.28	1.000
		Infrastructures <sup>2</sup>	-1.02	-1.91	-0.24	1.001
		Roads	-0.24	-1.25	0.76	1.000
		Roads <sup>2</sup>	0.64	-0.12	1.82	1.003
<b>Leopard</b>	<b>summer</b>	Cultivated	-1.14	-2.40	-0.10	1.001
		Forest	-0.31	-1.22	0.59	1.000
		Infrastructures	0.24	-0.82	1.36	1.001
		Infrastructures <sup>2</sup>	-1.20	-2.45	-0.16	1.000
		Roads	-0.76	-2.03	0.42	1.000
		Roads <sup>2</sup>	-0.75	-1.98	0.22	1.000
	<b>winter</b>	Cultivated	-0.42	-1.60	0.61	1.000
		Forest	0.35	-0.63	1.36	1.000
		Infrastructures	-0.24	-1.31	0.84	1.000
		Infrastructures <sup>2</sup>	-0.98	-2.12	-0.01	1.001
		Roads	0.25	-0.83	1.36	1.000
		Roads <sup>2</sup>	-0.55	-1.59	0.26	1.001
<b>Mesocarnivores</b>						
<b>Species</b>	<b>Season</b>	<b>Variables</b>	<b>Estimate</b>	<b>2.5 % CI</b>	<b>97.5 % CI</b>	<b>Rhat</b>
<b>Cape grey mongoose</b>	<b>summer</b>	Cultivated	-0.33	-1.10	0.39	1.001
		Forest	-1.07	-2.05	-0.18	1.000
		Infrastructures	-0.18	-1.05	0.64	1.000
		Infrastructures <sup>2</sup>	-0.27	-1.03	0.37	1.001
		Roads	0.14	-0.92	1.18	1.000
		Roads <sup>2</sup>	-0.73	-1.72	0.00	1.000
	<b>winter</b>	Cultivated	-0.79	-1.58	-0.02	1.000
		Forest	-0.76	-1.60	0.05	1.002
		Infrastructures	-0.48	-1.25	0.26	1.001
		Infrastructures <sup>2</sup>	-0.43	-1.13	0.19	1.000
		Roads	0.39	-0.61	1.40	1.000
		Roads <sup>2</sup>	-1.18	-2.21	-0.32	1.000
<b>Honey badger</b>	<b>summer</b>	Cultivated	-0.10	-0.94	0.73	1.002
		Forest	0.20	-0.64	1.08	1.001
		Infrastructures	-0.70	-1.66	0.20	1.000
		Infrastructures <sup>2</sup>	-0.71	-1.56	0.04	1.000

		Roads	-0.60	-1.65	0.45	1.000
		Roads <sup>2</sup>	-0.24	-1.13	0.60	1.000
	winter	Cultivated	-0.13	-1.04	0.88	1.000
		Forest	-0.47	-1.39	0.39	1.000
		Infrastructures	-0.23	-1.39	0.77	1.002
		Infrastructures <sup>2</sup>	-0.17	-1.07	1.03	1.000
		Roads	0.13	-1.09	1.32	1.000
		Roads <sup>2</sup>	-0.86	-2.02	0.19	1.002
<b>Large grey mongoose</b>	summer	Cultivated	-0.46	-1.46	0.47	1.000
		Forest	-0.39	-1.38	0.58	1.000
		Infrastructures	-0.55	-1.63	0.43	1.000
		Infrastructures <sup>2</sup>	-0.56	-1.47	0.20	1.000
		Roads	0.10	-1.08	1.19	1.000
		Roads <sup>2</sup>	-0.21	-0.89	0.31	1.001
	winter	Cultivated	-1.31	-2.55	-0.26	1.000
		Forest	-1.03	-2.05	-0.05	1.000
		Infrastructures	-0.08	-1.02	0.79	1.000
		Infrastructures <sup>2</sup>	-0.09	-0.84	0.68	1.000
		Roads	1.06	-0.06	2.26	1.000
		Roads <sup>2</sup>	-0.47	-1.08	0.25	1.002
<b>South African large-spotted genet</b>	summer	Cultivated	-0.66	-1.36	0.00	1.005
		Forest	-0.26	-1.00	0.43	1.003
		Infrastructures	-0.01	-0.69	0.68	1.000
		Infrastructures <sup>2</sup>	0.15	-0.39	0.81	1.000
		Roads	-0.02	-0.81	0.78	1.001
		Roads <sup>2</sup>	-0.12	-0.47	0.21	1.008
	winter	Cultivated	0.11	-0.59	0.85	1.003
		Forest	-0.40	-1.10	0.28	1.000
		Infrastructures	0.57	-0.09	1.23	1.001
		Infrastructures <sup>2</sup>	-0.13	-0.64	0.45	1.002
		Roads	1.33	0.41	2.23	1.000
		Roads <sup>2</sup>	0.18	-0.38	1.05	1.001
<b>Water mongoose</b>	summer	Cultivated	0.24	-0.47	0.96	1.000
		Forest	-0.38	-1.20	0.39	1.000
		Infrastructures	0.30	-0.45	1.09	1.000
		Infrastructures <sup>2</sup>	-0.05	-0.74	0.65	1.001
		Roads	0.24	-0.76	1.23	1.001
		Roads <sup>2</sup>	-0.63	-1.45	0.02	1.000
	winter	Cultivated	0.34	-0.44	1.21	1.000
		Forest	-0.04	-1.02	0.94	1.000
		Infrastructures	-0.32	-1.13	0.50	1.001
		Infrastructures <sup>2</sup>	0.60	-0.02	1.26	1.001
		Roads	0.39	-0.74	1.54	1.001
		Roads <sup>2</sup>	-1.70	-2.91	-0.63	1.002

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**Herbivores**


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Species	Season	Variables	Estimate	2.5 % CI	97.5 % CI	Rhat
Blue duiker	summer	Cultivated	-0.57	-1.53	0.29	1.001
		Forest	0.26	-0.44	0.97	1.000
		Infrastructures	0.27	-0.44	0.97	1.000
		Infrastructures <sup>2</sup>	-0.05	-0.67	0.50	1.001
		Roads	0.04	-0.84	0.89	1.000
		Roads <sup>2</sup>	0.00	-0.38	0.34	1.001
	winter	Cultivated	-0.28	-1.33	0.69	1.003
		Forest	0.96	0.14	1.86	1.002
		Infrastructures	0.05	-0.80	0.94	1.000
		Infrastructures <sup>2</sup>	-0.62	-1.56	0.14	1.001
		Roads	-0.08	-1.00	0.86	1.000
		Roads <sup>2</sup>	-0.49	-1.45	0.19	1.000
Bushbuck	summer	Cultivated	-0.10	-0.96	0.76	1.001
		Forest	0.14	-0.79	1.12	1.000
		Infrastructures	-0.05	-0.94	0.93	1.000
		Infrastructures <sup>2</sup>	0.20	-0.45	0.96	1.002
		Roads	-1.07	-2.22	0.03	1.001
		Roads <sup>2</sup>	0.51	-0.02	1.20	1.002
	winter	Cultivated	-0.11	-0.88	0.71	1.000
		Forest	0.21	-0.61	1.03	1.000
		Infrastructures	-0.39	-1.23	0.40	1.001
		Infrastructures <sup>2</sup>	0.12	-0.50	0.93	1.000
		Roads	0.35	-0.57	1.30	1.002
		Roads <sup>2</sup>	-0.24	-0.62	0.12	1.001
Cape grysbok	summer	Cultivated	-0.61	-1.84	0.54	1.002
		Forest	0.22	-0.78	1.35	1.000
		Infrastructures	-0.63	-1.80	0.44	1.001
		Infrastructures <sup>2</sup>	-0.18	-1.11	0.85	1.001
		Roads	0.80	-0.44	2.09	1.000
		Roads <sup>2</sup>	-0.71	-1.81	0.12	1.002
	winter	Cultivated	0.13	-0.76	1.00	1.002
		Forest	-0.26	-1.32	0.83	1.000
		Infrastructures	-0.30	-1.37	0.70	1.000
		Infrastructures <sup>2</sup>	0.21	-0.46	0.86	1.000
		Roads	1.02	-0.26	2.35	1.000
		Roads <sup>2</sup>	-1.21	-2.46	-0.24	1.002
Cape porcupine	summer	Cultivated	0.58	-0.10	1.31	1.001
		Forest	0.05	-0.67	0.81	1.000
		Infrastructures	-1.03	-1.82	-0.30	1.000
		Infrastructures <sup>2</sup>	-0.14	-0.69	0.40	1.000
		Roads	-0.24	-1.13	0.61	1.000
	winter	Roads <sup>2</sup>	-0.01	-0.37	0.34	1.000
		Cultivated	-0.10	-0.79	0.58	1.001
		Forest	-0.56	-1.29	0.15	1.000
		Infrastructures	-1.31	-2.03	-0.62	1.000

		Infrastructures <sup>2</sup>	-0.17	-0.71	0.44	1.000
		Roads	-0.32	-1.15	0.50	1.000
		Roads <sup>2</sup>	-0.05	-0.41	0.28	1.000
<b>Omnivores</b>						
<b>Species</b>	Season	Variables	Estimate	2.5 % CI	97.5 % CI	Rhat
<b>Bushpig</b>	summer	Cultivated	-0.65	-1.46	0.11	1.000
		Forest	-0.09	-0.86	0.64	1.000
		Infrastructures	-0.77	-1.80	0.03	1.000
		Infrastructures <sup>2</sup>	0.10	-0.55	1.01	1.001
		Roads	-0.07	-1.01	0.88	1.000
		Roads <sup>2</sup>	0.11	-0.49	1.02	1.001
	winter	Cultivated	0.32	-0.35	1.06	1.000
		Forest	1.01	0.28	1.78	1.000
		Infrastructures	-0.66	-1.38	0.02	1.002
		Infrastructures <sup>2</sup>	-0.08	-0.57	0.45	1.000
		Roads	-0.90	-1.86	0.01	1.002
		Roads <sup>2</sup>	0.40	0.01	0.91	1.001
<b>Chacma baboon</b>	summer	Cultivated	-0.07	-0.78	0.63	1.000
		Forest	0.41	-0.30	1.16	1.001
		Infrastructures	-0.95	-1.73	-0.23	1.001
		Infrastructures <sup>2</sup>	-0.38	-0.91	0.14	1.003
		Roads	0.27	-0.58	1.14	1.001
		Roads <sup>2</sup>	-0.01	-0.34	0.41	1.001
	winter	Cultivated	-0.10	-0.77	0.55	1.002
		Forest	-0.04	-0.73	0.65	1.000
		Infrastructures	-0.62	-1.31	0.04	1.000
		Infrastructures <sup>2</sup>	-0.06	-0.57	0.46	1.000
		Roads	-0.29	-1.19	0.57	1.000
		Roads <sup>2</sup>	-0.59	-1.40	0.03	1.000
<b>Vervet monkey</b>	summer	Cultivated	0.02	-0.67	0.74	1.000
		Forest	-0.09	-0.84	0.69	1.001
		Infrastructures	-0.50	-1.34	0.31	1.000
		Infrastructures <sup>2</sup>	-0.55	-1.25	0.07	1.003
		Roads	0.40	-0.50	1.29	1.001
		Roads <sup>2</sup>	-0.31	-0.86	0.12	1.001
	winter	Cultivated	-0.07	-0.77	0.64	1.000
		Forest	-0.76	-1.57	0.01	1.000
		Infrastructures	-0.35	-1.13	0.39	1.001
		Infrastructures <sup>2</sup>	-0.45	-1.10	0.12	1.000
		Roads	0.78	-0.11	1.76	1.001
		Roads <sup>2</sup>	-0.50	-1.13	-0.04	1.000

**TABLE S3** Summary table of the p-values values for each model.

<b>Species</b>	<b>Winter</b>	<b>Summer</b>
Blue duiker	0.42	0.38
Bushbuck	0.43	0.33
Bushpig	0.51	0.52
Cape grey mongoose	0.51	0.51
Cape grysbok	0.48	0.66
Caracal	0.59	0.62
Chama baboon	0.48	0.41
Honey badger	0.61	0.56
Large grey mongoose	0.65	0.46
Large-spotted genet	0.45	0.46
Vervet monkey	0.48	0.42
Leopard	0.62	0.55
Porcupine	0.39	0.46
Water mongoose	0.53	0.54

**TABLE S4** Summary table of the BIC values for each model.

<b>Species</b>	<b>Winter</b>	<b>Summer</b>
Blue duiker	267.2	313.4
Bushbuck	1446.8	1492.3
Bushpig	838.7	694.2
Cape grey mongoose	269.7	180.3
Cape grysbok	89.2	71.9
Caracal	324.1	266.3
Chama baboon	473.7	499.3
Honey badger	249.3	282.0
Large grey mongoose	119.5	98.2
Large-spotted genet	1015.8	967.2
Vervet monkey	296.8	270.0
Peopard	109.6	126.9
Porcupine	636.3	478.7
Water mongoose	218.9	244.9

**TABLE S5** Summary table of the number of detection for each species in the grouped by areas with high and low road length.

<b>Species</b>	<b>High density</b>	<b>Low density</b>
Bushbuck	11383	12502
Chacma baboon	2768	1475
Porcupine	865	1994
Vervet monkey	862	870
Bushpig	806	1584
Blue duiker	596	451
Large-spotted genet	462	1824
Cape grey mongoose	143	170
Caracal	113	282
Leopard	89	34
Honey badger	87	165
Water mongoose	18	334
Large grey mongoose	11	93
Cape grysbok	6	248
Humans	2486	7680

**TABLE S6** Summary table of the number of detection for each species in the grouped by areas close and far from human infrastructure.

<b>Species</b>	<b>Close to infrastructure</b>	<b>Far from infrastructure</b>
Bushbuck	20474	3411
Chacma baboon	4079	164
Porcupine	2796	63
Vervet monkey	1615	117
Bushpig	1726	664
Blue duiker	658	389
Large-spotted genet	1486	800
Cape grey mongoose	211	102
Caracal	313	82
Leopard	104	19
Honey badger	213	39
Water mongoose	263	89
Large grey mongoose	97	7
Cape grysbok	254	0
Humans	8091	2075

**TABLE S7** Overlap value for each species between areas with high and low road length.

<b>Species</b>	<b>Overlap</b>
Chacma baboon	0.658
Bushbuck	0.867
Bushpig	0.923
Caracal	0.803
Blue duiker	0.818
Large-spotted genet	0.902
Honey badger	0.721
Leopard	0.781
Cape grey mongoose	0.797
Vervet monkey	0.819
Porcupine	0.885
Humans	0.808

**TABLE S8** Overlap value for each species between areas close and far from human infrastructure.

<b>Species</b>	<b>Overlap</b>
Chacma baboon	0.625
Bushbuck	0.827
Bushpig	0.846
Caracal	0.749
Blue duiker	0.793
Large-spotted genet	0.899
Honey badger	0.548
Cape grey mongoose	0.753
Vervet monkey	0.856
Porcupine	0.772
Water mongoose	0.853
Humans	0.736



## Chapter 2

### Using a citizen approach to monitor African mammals in multifunctional landscapes



As there are many private properties in the GRBR, which are not easily accessible to do biodiversity monitoring, we evaluated the potential of using LEK to inform mammals human-dominated habitats use. This method enabled to have a larger spatial coverage with a low-cost protocol than the CTs set-up. Furthermore, it is a way of integrating residents into the research process. We obtained 247 responses that were consistent with the results obtained from the CTs analyses (manuscript 2) and showed that the use of human-dominated habitats was species-dependent. Some species such as the chacma baboon were attracted to anthropogenic resources, while dependence on natural habitats was still evident for the blue duiker. The results suggest the positive effect of preserving patches of natural vegetation on private property for mammal conservation. The survey enabled us to describe the anthropogenic resources available on human properties, which was missing in the CTs analysis. Furthermore, LEK provided more accurate information than CTs on local practices and wildlife perceptions. The following paper has not been peer-reviewed yet.

Manuscript associated to chapter 2:

- Manuscript 3: **Alice Bernard**, Hervé Fritz, Jan A. Venter, Chloé Guerbois. A local ecological knowledge-based assessment of anthropodependence for large mammals in anthropogenic landscapes

## Manuscript 3

# A local ecological knowledge-based assessment of anthropodependence for large mammals in anthropogenic landscapes

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## Abstract

Humans have substantially changed the environment through landscape transformation, disturbance, and resource exploitation, leading to major habitat loss. Human and wildlife cohabitation could be a means of preventing biodiversity loss. Mammal species are highly diverse and are thus not expected to respond uniformly to human disturbance. It is essential to understand how mammals persist in human-dominated landscapes and what influences their presence, to apply relevant conservation measures. The Garden Route District Municipality of South Africa, a mosaic landscape where human activities and wildlife meet, is an ideal site to examine how anthropogenic disturbance influences wildlife occurrence. To maximise our area coverage through a replicable, low-cost protocol, we designed an online survey aimed at private landowners to investigate the effect of landscape metrics and property attributes — such as the availability and type of anthropogenic resources, the integrity and type of natural habitats, structural disturbances and interferences — on the persistence of wild mammals in such environments. We collected data from 247 respondents to investigate the occurrence of 14 mammal species. Species exhibited unique responses to anthropogenic variables. Our results demonstrated the negative impact of human footprints, but also the positive role of residents in protecting mammals by preserving patches of natural vegetation on their properties as a counterbalance to habitat destruction and fragmentation. Local ecological knowledge should be used to document mammal persistence in human-dominated mosaic landscapes, as it provides information on local practices and allows researchers to engage indirectly with a wide variety of stakeholders.

**Key words:** Online survey, mammal ecology, participatory method, habitat transformation, biosphere reserve, anthropogenic landscapes

## 1 | Introduction

Humans have altered the majority of terrestrial land during the last 12,000 years (Ellis et al., 2021), inducing the transformation of 58% of terrestrial ecosystems (Williams et al., 2020). Human-wildlife coexistence constitutes a major challenge, as 25% of mammal species are threatened as a result of human activities, such as habitat alteration and resource use (Diaz, 2019). Protected areas are a widespread approach to conservation, although their effectiveness is sometimes contested and context-dependent (Craigie et al., 2010; Gatiso et al., 2022; Geldmann et al., 2019). Because of the diversity of species home-ranges and ecological requirements, as well as the challenge of protecting intact areas from human activities, researchers have called for more consideration of spaces 'shared' between humans and wildlife and methods of improving their coexistence (Obura et al., 2021; Rosenzweig, 2003). The purpose of these shared areas is to connect people and nature rather than separate them, while designing more wildlife-friendly habitats to complement strictly protected areas (Obura et al., 2021). Biosphere reserves and transboundary conservation areas are recent governance models that aim to combine socio-economic dimensions and biodiversity conservation in protected areas and their surroundings (Bourgeois et al., 2023; Pool-Stanvliet & Coetzer, 2020). Some research has indicated that coexistence between large mammals and humans in anthropogenic landscapes is possible. For instance, Cretois et al. (2021) found that, in Europe, biophysical factors such as evapotranspiration, snow cover duration and terrain relief had a greater influence on species distribution than anthropogenic constraints. Predators, such as mammals (foxes and caracals) or birds (sparrows), are good examples of species that benefit from human landscape transformation by preying on species commensal to humans, such as rodents or domestic animals (Fleming & Bateman, 2018; Natrass & O'Riain, 2020).

Not all wild mammal species are expected to exhibit the same responses to anthropogenic disturbances, habitat modification and other ecological impacts. Some species may not succeed in anthropogenic environments (Sebastián-González et al., 2019), while others may thrive because of novel predation opportunities or refuge (Fleming & Bateman, 2018), which could be attributed to specific traits (Santini et al., 2019). Modifying of spatio-temporal niche partitioning is a common outcome of mammal adaptation to anthropogenic disturbances (Sévêque et al., 2020). Sévêque et al. (2020) reviewed the influence of human disturbances on the spatial, temporal and niche overlap between carnivore communities. They grouped human disturbances into two categories: top-down disturbances, corresponding to direct human presence (e.g., recreational activities, hunting and pets), and bottom-up disturbances, corresponding to land modification (e.g., built-up environments and agricultural land uses). Both types of disturbance often have negative consequences for wild mammal habitat use (Larson et al., 2016; Nickel et al., 2020). Sometimes, these effects can be contradictory, which underlines the importance of considering these two forms of human disturbance separately when evaluating anthropogenic impacts on wildlife (Nickel et al., 2020; Sévêque et al., 2020). Species can adapt by shifting to nocturnality, which can have numerous consequences, such as a dietary shift to nocturnal prey, exposure to new predators or diminution of conflict with humans (Gaynor et al., 2018). Species often also modify their diet in anthropogenic environments in response to different resource availability (Drouilly et al., 2018; Leighton et al., 2022). Hulme-Beaman et al. (2016) proposed a framework for classifying the responses of species populations to anthropogenic contexts according to their home-range overlap with

anthropogenic environments and anthropogenic resource consumption. The term 'commensal' reflects a capacity for exploiting a new environment, but no associated impact on humans. Because it is rarely the case, human-dominated environments, Hulme-Beaman et al. (2016) introduced the term 'anthropodependent'.

Research on mammal responses to anthropogenic landscape transformation has mainly focused on data based on ecological approaches, such as camera trap surveys and movement or diet studies (Drouilly et al., 2018; Ngcobo et al., 2019; Nickel et al., 2020). In a mosaic of landscapes and ecosystems such as the Garden Route in South Africa, where private and public landowners share multiple boundaries and interfaces with natural, agricultural and urban areas, it might be challenging to set up monitoring protocols. In this heterogeneous context, participatory approaches offer potentially valuable methods of gathering information on landowners' practices as well as wildlife presence. Participatory methods have elicited concerns over the accuracy of the data collected, such as species identification, location and timing, which requires time investment to ensure adequate quality (Devictor et al., 2010; Young et al., 2019). However, studies have also demonstrated the benefits of using participatory approaches (Bennett et al., 2017; Devictor et al., 2010). These approaches have been used to collect various information, which has provided insight into conservation practices from the global to local scale and supported the investigation of narratives, governance systems, values and perceptions surrounding conservation (Bennett et al., 2017). Although an increasing number of studies are using large-scale citizen science (Dickinson et al., 2012; Swanson et al., 2015; Young et al., 2019), few have focused on collecting information on mammal species occurrence using participatory approaches (Burt et al., 2021; Dickinson et al., 2012; Pédarros et al., 2020). Questionnaire-based surveys are a potential tool to study human-wildlife interactions, allowing for the collection of a large amount of data on human practices and perceptions of their environment (White et al., 2005).

The aim of this study was to understand better how mammal species persist in anthropogenic landscapes and what factors influence their occurrence, using data based on local ecological knowledge. Mammals vary in weight (500 g to 52 kg in the case of this study), ecology, life history traits and trophic positions. Some mammals have adapted to urban spaces, either permanently or intermittently, and thus serve as good indicators of ecosystem disturbance, which is why we have focused on this taxon for this study (Santini et al., 2019). We used as a theoretical framework a combination of the conceptual models proposed by Hulme-Beaman et al. (2016) and Sévêque et al. (2020), which we tested using data gathered from private landowners. The study was conducted in the Garden Route Biosphere Reserve, a mosaic landscape that forms part of the Cape Floristic Region (Weinzettel et al., 2018), where remnant patches of Afrotropical Forests have been conserved in formally protected areas over the past 15 years.

## 2 | Materials and methods

### 2.1 | Study area

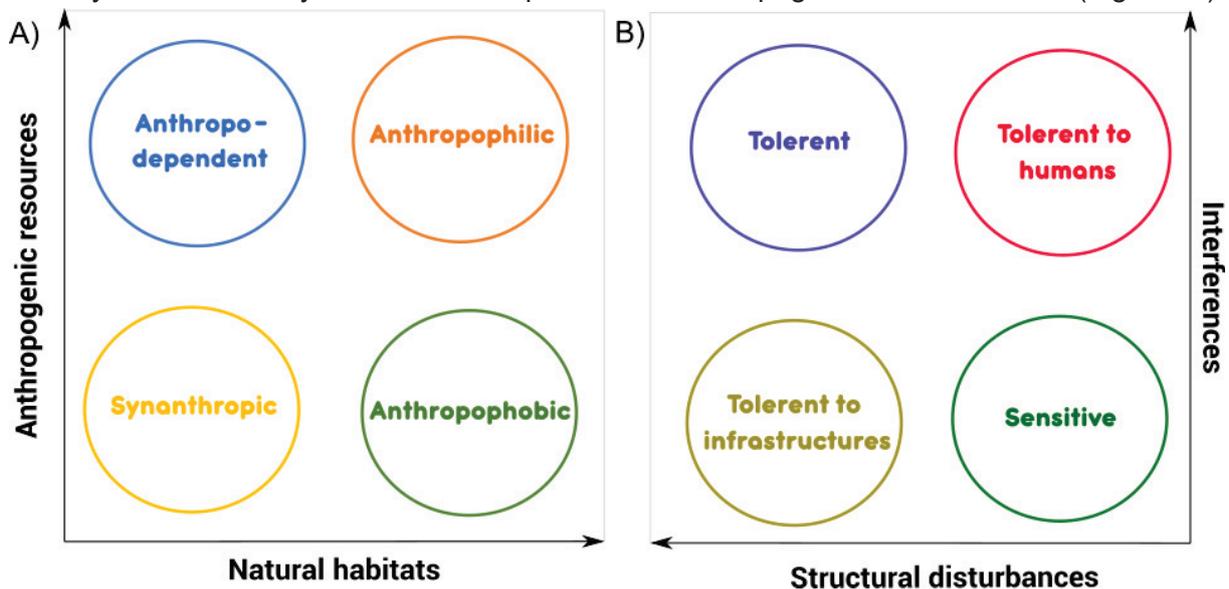
The study area is located in the Garden Route District Municipality (GRDM), on the south-eastern coast of South Africa, between the Indian Ocean and Outeniqua mountains, and

covers an area of approximately 700,000 ha. The area includes a variety of biomes, such as Afrotropical Forest, diverse types of fynbos as well as wetland, riverine and coastal habitats (Baard et al., 2015; SANParks, 2020). Since 1930, the number of suburbs and residences within the study area has increased drastically (Crisp, 2015) and the population is expected to keep growing (Western Cape Government, 2019). As of 2019, the population of the GRDM was 620,000 (Western Cape Government, 2019), with a population density of approximately 27 persons/km<sup>2</sup> (Western Cape Government, 2019). Anthropogenic landscape transformation is associated with multiple land uses, such as forest plantations, crops, dairy farming, urban and peri-urban development and vast road networks (SANParks, 2020). The Garden Route National Park, a non-fenced protected area managed by South African National Parks (SANParks) and covering 5% of the GRDM (23,331 km<sup>2</sup>), was established in 2009 with the primary objective of protecting remnant patches of indigenous forest. The Garden Route Biosphere Reserve is the ninth in South Africa to be recognised by UNESCO (Pool-Stanvliet & Coetzer, 2020). In addition to these formally protected areas, Critical Biodiversity Areas are identified in the Western Cape Biodiversity Spatial Plan Handbook (CapeNature, 2017) as those required to achieve ecosystem and species conservation objectives.

## 2.2 | Study design

### 2.2.1 | Conceptual framework

This study used the framework for anthropodependence proposed by Hulme-Beaman et al. (2016), combined with that for human disturbances developed by Sévêque et al. (2020), to classify the sensitivity of mammal species to anthropogenic environments (Figure 1).



**FIGURE 1** A) Conceptual framework for land uses and resources, adapted from Hulme-Beaman et al. (2016). Anthropodependent species consume human food resources and occupy human habitats; anthropophilic species regularly consume anthropogenic resources, but do not occupy human habitats; synanthropic species have home-ranges that overlap with anthropogenic environments, but do not consume anthropogenic resources; and anthropophobic neither occupy human habitats nor consume human resources. B) Conceptual framework for human disturbances, adapted from Sévêque et al. (2020). Interferences correspond to top-down disturbances, whereas structural disturbances correspond to bottom-

up disturbances. Tolerant species (high interference and structural disturbance) correspond to anthropodependent species; species tolerant to humans but not infrastructure (high interference, low structural disturbance) are more likely to broadly correspond to anthropophilic species; species tolerant to humans but not infrastructure (low interference, high structural disturbance) correspond broadly to synanthropic species; and sensitive species (low interference, low structural disturbance), which cannot come into contact with humans or related infrastructure, are likely to be anthropophobic.

### 2.2.2 | Data collection

We used a local ecological knowledge-based approach to test the frameworks described in Section 2.2.1 (Figure 1). Questionnaire was designed to achieve the following objectives: 1) assess mammal species occurrence in human-dominated landscapes, 2) gather information on property characteristics and landscape elements and 3) obtain information about participants, such as ecological knowledge. The questionnaire was piloted face-to-face and online with 20 volunteers and subsequently revised. The final questionnaire consisted of nine parts and 59 questions, most of which were multiple-choice to avoid subjective interpretation. The survey was administered through the platform SurveyMonkey, and the questionnaire is accessible in **Appendix 1**. The survey targeted landowners in the GRDM, as most properties in the area are privately owned. We used a random sampling method and sent the questionnaire to mailing lists obtained from CapeNature, SANParks, the Wildlife and Environment Society of South Africa and local conservancies. We also posted the link to the questionnaire on multiple WhatsApp and Facebook groups of the different Local Municipalities to reach the largest audience possible. Lastly, we published the link to the questionnaire in local newspapers (*George Herald* and *The Edge*). The questionnaire was available in English and Afrikaans, as these are the two most spoken languages among landowners in the study area. The survey was accessible online from November 2021 to March 2022. To preserve their anonymity, participants were asked to indicate the general location of their property on a cell of 2.23 \* 2.23 km on a map. This research was approved by the Nelson Mandela University Research Ethics Committee (H20-SCI-SRU-002).

### 2.2.3 | Data processing

#### 2.2.3.1 | *Property characterisation*

To test the conceptual framework and accurately describe the diversity of properties, we used variables measured by 12 questions in the questionnaire to build a gradient for each of the following dimensions of the conceptual model: anthropogenic resources, natural habitats, structural disturbances and interferences (Figure 1). The questions and associated variables used are listed and described in Table S1.

First, to describe anthropogenic resources, we gathered information on land-uses (pastures, crops, orchards, vegetable gardens and exotic tree plantations), domestic animals (small livestock — goats, pigs and sheep — cattle and poultry) and waste management. Each of these variables was assigned a binary value of either 0 (absent) or 1 (present) per property. All variables that exhibited less than 10% variability (> 90% of either 1 or 0) were excluded from subsequent analyses. We built a resource index for each property by summing all the available resources, as we hypothesised that properties with higher resource diversity would

attract more species. We obtained a numerical value from 0 to 15, representing the number of different resources. We assigned the available resources per property one of three values: 0 (no resources), 1 (resources present) or 2 (resources easily accessible). Resources considered as easily accessible to wildlife corresponded to resources on properties that had previously sustained damages. Second, because our default focus was fairly modified, anthropogenic landscapes, we chose to build a gradient of natural habitats rather than modified habitats. We recorded the presence of natural habitats as well as their state, and assigned a given habitat (wetland, riverine, scrub forest, Afrotropical Forest, thicket and fynbos) a value of either 0 (absent), 1 (present but disturbed or under rehabilitation) or 2 (present and in its natural state). We calculated habitat diversity by summing the number of habitats present on each property and obtained a numerical value ranging between 0 and 6. Third, to assess structural disturbances, we calculated the total length of roads in each 2.23 \* 2.23 km cell to measure the level of urbanisation ('st\_intersection' and 'st\_length'; functions 'sf' package) (Pebesma, 2018). Furthermore, we considered fences, as a categorical variable (presence or absence), and the proportion of each property excluding wildlife, as a numerical variable, as additional measures of infrastructural disturbance. Fourth, to assess potential interferences, we used the binary variable of intentional killing (hunting, dog hunting, snaring and poaching), assigned a value of either 1 (present) or 0 (absent); the average number of people present; the number of dogs present; and a categorical variable describing the extent of dog presence (present across the whole property, excluded from a portion of the property or completely absent).

We conducted multivariate analyses using the variables described above to build the four gradients. We performed a principal component analysis of the anthropogenic resource and natural habitat gradients (Figure S1) and a Hill and Smith analysis (Figure S2) of the structural disturbance and interference gradients ('dudi.pca' and 'dudi.hillsmith' functions respectively, 'ade4' package) (Dray & Dufour, 2007).

### 2.2.3.2 | Species characterisation

Species presence was assessed by a multiple choices questions (e.g., 'At what frequency do the following species occur on your property?', not anymore, rarely, occasionally, frequently, very frequently). Because mongooses and genets were difficult to distinguish, we used the general categories 'mongooses' (including the Cape grey mongoose, *Herpestes pulverulentus*, large grey mongoose, *Herpestes ichneumon* and water mongoose, *Atilax paludinosus*) and 'genets' (including the large-spotted genet, *Genetta tigrina* and small-spotted genet, *Genetta genetta*) in subsequent analyses. Respondents could select these general categories when they did not know the differences between these species. Only the large-spotted genet has been recently recorded in the area, although both species are listed as potentially occurring (Baard et al., 2015). Respondents were also asked how they detected species presence on their properties (sightings, tracks, scats, hair, sounds, feeding signs, burrows, species carcasses, camera traps, word of mouth or other signs). We transformed occurrence frequency responses to obtain a presence/absence variable that encompassed more than 10% of responses indicating the presence of rare species or absence of abundant species. When a respondent did not answer the question or reported that a species no longer occurred on their property, we assigned the variable a value of 0 (absence). When a species occurred very

frequently, frequently, occasionally or rarely, we assigned the variable a value of 1 (presence) (Table S1).

### 2.2.3.3 | Additional variables

To assess the ecological knowledge of the respondents, we asked four questions. Two were based on identifying a species using a photograph: a herbivore (blue duiker, *Philantomba monticola*) and mesocarnivore (Cape mongoose). The third required respondents to identify the track of a carnivore (caracal, *Caracal caracal*), and the fourth to identify the scat of a herbivore (porcupine, *Hystrix africaeaustralis*). For each question, respondents were given a choice of three species. To assess the diversity of landscapes covered by the survey, we calculated the mean Human Modification Index (HMI), a value in the continuous range of 0–1, of each 2.23 \* 2.23 km cell, where a value close to 0 indicated no modification and a value close to 1 indicated very high modification (Kennedy et al., 2020). To estimate respondent bias linked to the proximity of protected areas, we calculated the mean distance of the centroid of each 2.23 \* 2.23 km cell to the GRNP border, using a shapefile obtained from SANParks (Baard et al., 2015). Respondents were asked whether they were part of any conservation initiatives, in order to further assess the potential bias of people interested in the study. Respondents were given the options of conservancy, non-profit organisation (NPO), non-governmental organisation (NGO), other conservation body or no conservation initiatives. The responses in the 'other' category were manually reclassified, as some respondents specified the initiatives with which they were involved.

## 2.3 | Data analyses

To derive relevant property characterisation variables, we first tested the correlation between the eight synthetic variables obtained from the four different multivariate analyses (Figure S3), using the 'cor' function and 'stats' package (R Core Team, 2020). As they were not correlated, we used all eight synthetic variables for the following analyses. To model the number of species per property and the occurrence of each species, we ran a generalised linear model with a normal and binomial distribution, respectively, using the eight synthetic property characterisation variables. We then performed a dredge procedure and selected the best models with a cumulative weight of 95%. We averaged the best models (using the 'dredge' and 'model.avg' functions and 'MuMIn' package) and stored the estimates of the conditional model. We calculated the 95% confidence interval of each estimated value ('confint' function, 'stat' package). We then calculated the sum of the Akaike weights of the recorded species ('sw' function, 'MuMIn' package) to determine the importance of the eight synthetic variables (Barton, 2022). Finally, we calculated the predicted values of species occurrence probability as well as the standard error of our model average ('predict' function, 'car' package) (Fox & Weisberg, 2019). All analyses were performed using R (R Core Team, 2020). We used the 'ggplot2' package for graphical representation (Wickham, 2016).

## 3 | Results

We received a total of 262 participations, of which only 247 were complete. These included respondents from several Local Municipalities (55 from Bitou, 110 from George, 72 from

Knysna and 8 from Mossel Bay; Table S4), who had lived in the GRDM for an average of 11.85 years. Most of the respondents were involved in conservation initiatives (37% were part of a conservancy, 32% of an NPO and 10% of an NGO), whereas only 2% were not. The respondents lived in a spectrum of urban, rural and natural areas, as demonstrated by the HMI value which ranged from 0.1 to 0.86, with an average value of 0.39. The distance between the respondents' properties and the GRNP ranged from 0 to 52.3 km, with an average of 3 km.

### 3.1 | Species characterisation

Only one third of respondents obtained an ecological knowledge score (based on species, track and scat identification) above 75%, and one third under 25% (Figure S5). The best results were obtained when identifying a species based on a photograph; 83% correctly recognised the blue duiker, and 59% the Cape mongoose. In contrast, only 36% identified the caracal track, and 27% the porcupine scat. Most respondents confirmed the presence of species on their properties by sightings (Table S2).

We obtained records for 25 different mammal species but given the relatively low ecological knowledge scores, we only included the 14 most commonly recorded species (Tables 2 and S6, Figure S7), which we expected the highest ecological knowledge levels as these 14 species were identified by more than 10% of the respondents. An average of six different species were recorded per property (Figure S6). Very common species included the bushbuck (80%), porcupine (72%) and vervet monkey (71%). Rarer species (recorded on less than 25% of properties) included the blue duiker, Cape grysbok, leopard, African clawless otter and common duiker (Table 1).

**TABLE 1** Summary of the 14 most recorded species. Icons were downloaded from [www.phylopic.org](http://www.phylopic.org)

English name		Order	Family	Scientific name	Percentage of properties where the species was present
Bushbuck		Artiodactyla	Bovidae	<i>Tragelaphus scriptus</i>	80%
Cape porcupine		Rodentia	Hystricidae	<i>Hystrix africaeaustralis</i>	72%
Vervet monkey		Primates	Cercopithecidae	<i>Chlorocebus pygerythrus</i>	71%
Mongoose: Cape grey mongoose, large grey mongoose, water mongoose		Carnivora	Herpestidae	<i>Herpestes pulverulentus</i> , <i>Herpestes ichneumon</i> , <i>Atilax paludinosus</i>	67%
Chacma baboon		Primates	Cercopithecidae	<i>Papio ursinus</i>	57%
Caracal		Carnivora	Felidae	<i>Caracal caracal</i>	55%
Bushpig		Artiodactyla	Suidae	<i>Potamochoerus larvatus</i>	54%
South African large-spotted genet		Carnivora	Viverridae	<i>Genetta tigrina</i>	43%
Honey badger		Carnivora	Mustelidae	<i>Mellivora capensis</i>	35%
African clawless otter		Carnivora	Mustelidae	<i>Aonyx capensis</i>	21%
Common duiker		Artiodactyla	Bovidae	<i>Sylvicapra grimmia</i>	21%
Leopard		Carnivora	Felidae	<i>Panthera pardus</i>	21%
Cape grysbok		Artiodactyla	Bovidae	<i>Raphicerus melanotis</i>	19%
Blue duiker		Artiodactyla	Bovidae	<i>Philantomba monticola</i>	15%

### 3.2 | Property characterisation

Respondents engaged in different types of agricultural activities, such as commercial farming (6.5%), subsistence farming (10.5%) and home gardening (26.3%). The presence of dogs was reported on 71% of properties. The majority of respondents (67%) had dogs for company, whereas only 13 respondents (0.7%) had dogs to protect their houses from wildlife. Fences were present on 82.6% properties, of which 58% were only partially fenced. Only 17.4% of properties did not have any fences. Respondents had fences for one or more reasons, such as keeping wildlife out (5.6%), keeping domestic animals in (47%), protecting crops (20%), preventing crime (30%) or because the fences were already there when they moved onto the property (24%).

The multivariate analyses allowed us to create eight synthetic variables, describing the four gradients used to classify the properties of respondents according to the availability and type of anthropogenic resources (from farming to residential); the diversity and type of natural habitats, based on a hydromorphic gradient (from wetlands to fynbos); an urbanisation gradient and level of connectivity; and different kind of interferences, from dogs or humans (Table 2, Figures S1, S2 and S8).

**TABLE 2** Results of the multivariate analyses used to construct gradients of anthropogenic resources, natural habitats, structural disturbances and interferences. Based on the percentage of inertia, we only kept the first two principal axes as new synthetic variables for subsequent analyses.

Gradient	Variables used	Axis	Inertia	Percentage of inertia	Synthetic variables	Definition
<b>Anthropogenic resources</b>	Presence and accessibility of modified habitats, domestic animals, rubbish and compost; damages; number of resources	1	4.1203	37.46	Availability	Diversity and availability of anthropogenic resources
		2	1.6167	14.69	Farming vs residential)	Positive values describe more farming properties (livestock, poultry and pasture), whereas negatives values represent more residential areas (vegetable gardens, rubbish and compost)
<b>Natural habitats</b>	Presence and state of natural habitats; number of natural habitats	1	3.0828	44.04	Diversity and integrity	Diversity and integrity of natural habitats
		2	1.0877	15.54	Hydromorphy	Positive values describe properties with wetlands, whereas negative values describe properties with drier habitats, such as thicket and fynbos. Values around zero represent properties with forests and riverine habitats.
<b>Structural disturbances</b>	Fences; road length; proportion excluding wildlife	1	1.5174	50.58	Human footprint	Positive values describe properties that exclude wildlife and are surrounded by a long road network
		2	0.988	32.93	Connectivity	Positive values describe properties without fences, whereas negative values represent properties with fences.
<b>Interferences</b>	Intentional killing; number of people; number of dogs; exclusion of dogs	1	1.6435	32.87	Dogs	Number of dogs
		2	1.1499	23.00	Humans	Positive values are linked to the number of people and the presence of hunting activities (dog hunting, hunting, snaring and poaching)

### 3.3 | Community responses to anthropogenic variables

The availability of anthropogenic resources was the most significant synthetic variable in predicting the diversity of species on private properties ( $P < 0.05$ ), followed by the diversity and integrity of natural habitats ( $P < 2e-06$ ) and the presence of dogs ( $P = 0.008$ ). Species diversity declined with increasing human footprint ( $P < 8e-07$ ). The other synthetic variables were not significant (Figure S9, Table S4).

### 3.4 | Species responses to anthropogenic variables

Species showed different responses to anthropogenic variables (Figure 2). With the highest summed Akaike weight values, diversity of natural habitats (10.8), urbanisation (10.7) and availability of anthropogenic resources (10.6) were the main synthetic variables determining the presence of mammal species on private properties in the GRDM (Figure 2, Table S5). They were followed by dogs (7.5), connectivity (7.3), hydromorphy (6.8), type of anthropogenic resource (farming vs residential; 6.7) and humans (4.5). The predicted values, represented only for the three most important synthetic variables, showed different patterns between species (Figure S10). Subsequent analyses and interpretation only focused on the synthetic variables with significant effects.

#### 3.4.1 | Anthropogenic resources

The accessibility of anthropogenic resources was the most important synthetic variable in predicting the presence of the following five mammal species: baboon, bushpig, bushbuck, honey badger and otter. All species except for the grysbok, blue duiker, leopard and mongooses were significantly correlated with the availability and accessibility of anthropogenic resources (Figure 2). The probabilities of genet and caracal occurrence tended to increase with increasing anthropogenic resources availability. Herbivores were split into two groups: those positively associated (bushbuck and porcupine) and those negatively associated (common duiker) with anthropogenic landscapes. The probabilities of otter and honey badger occurrence increased with the increasing availability of anthropogenic resources. The probability of occurrence of all omnivores also increased with the increasing availability of anthropogenic resources and natural habitats. However, the probability of baboon and bushpig occurrence started lower higher than that of vervet monkeys, suggesting that baboons and bushpigs were more likely to be present on properties where anthropogenic resources were available (Figure S10A). The farming-residential gradient was significant only for herbivores ( $P < 0.05$ ): the blue duiker, common duiker and grysbok. All were more likely to be found in residential areas than in farming areas (Figure 2, Table S5). However, the variable was the most important determining factor of only the common duiker.

#### 3.4.2 | Natural habitats

All 14 species occurred more on properties with natural habitats. This synthetic variable significantly correlated with nine species (all carnivores and omnivores) and was the most important determinant for seven (Figure 2, Table S5). Genets, otters and mongooses (mesocarnivores) as well as the grysbok and common duiker (herbivores) were not significantly attracted to the diversity of natural habitats (Figure 9B). The hydromorphy of natural habitats was not the most important synthetic variable for any species. However,

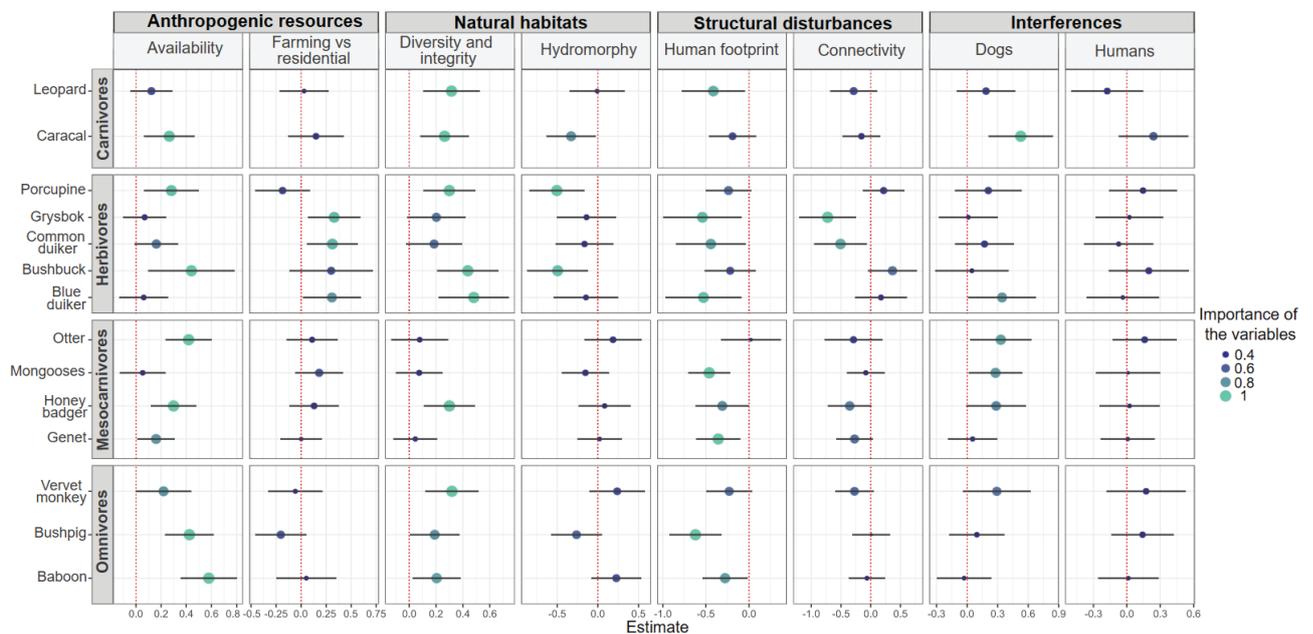
caracal, porcupine and bushbuck ( $P < 0.05$ ) tended to select for dryer areas (Figure 2, Table S5).

### 3.4.3 | Structural disturbances

Human footprint was the most important synthetic variable for four species and had a significant effect on the occurrence of eight ( $P < 0.05$ ). The probability of occurrence of all these species decreased with increasing human footprint (Figures 2 and S10C, Table S5). All other species showed relatively linear negative trends, except the bushpig, which showed a drastic decline with increasing urbanisation. In contrast, mongooses appeared to tolerate a higher level of urbanisation than other species before declining (Figure 10C). Connectivity significantly correlated only with the two herbivores — the grysbok and common duiker ( $P < 0.05$ ) — and was the most important synthetic variable for the former. These species were negatively correlated with connectivity, *i.e.*, properties with fences (Figure 2, Table S5).

### 3.4.4 | Interferences

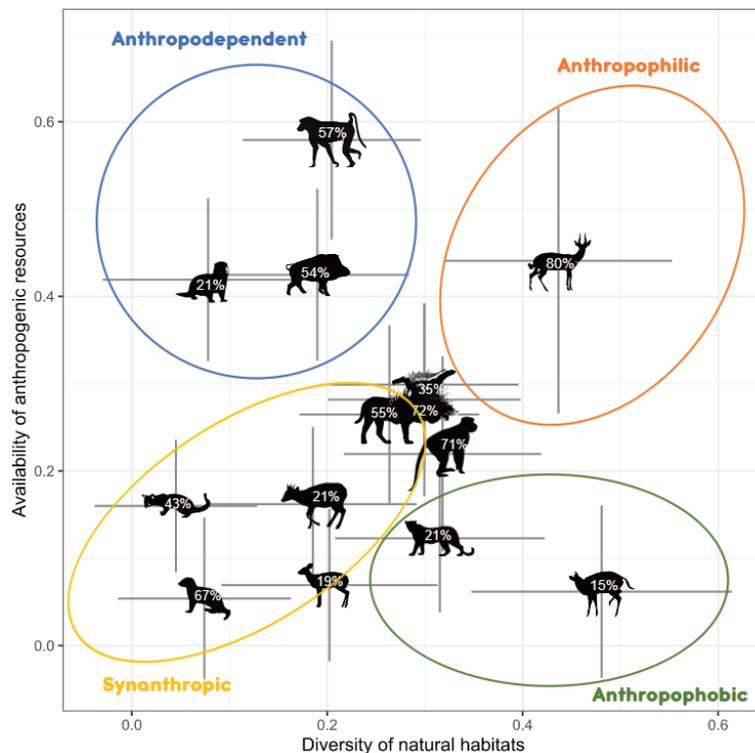
The presence of dogs was the most important variable in predict the occurrence of caracals. Additionally, the caracal, blue duiker, otter, mongoose and honey badger were significantly associated with the presence of dogs (Figure 2, Table S5). None of the species significantly correlated with human interference (Figure 2, Table S5).



**FIGURE 2** Standardised estimates of the generalised linear models (gradient of blue) per species in relation to the eight synthetic variables. Species are sorted by diet type. Larger points in blue/green represent more important synthetic variables (greater sums of Akaike weights). Black lines represent the 95% confidence interval for each estimated value. Red lines highlight the position of 0 on the x-axis. If the confidence interval of a variable excludes 0, the variable is significant. The further away from 0, the greater the estimate.

### 3.5 | Testing the anthropodependence framework

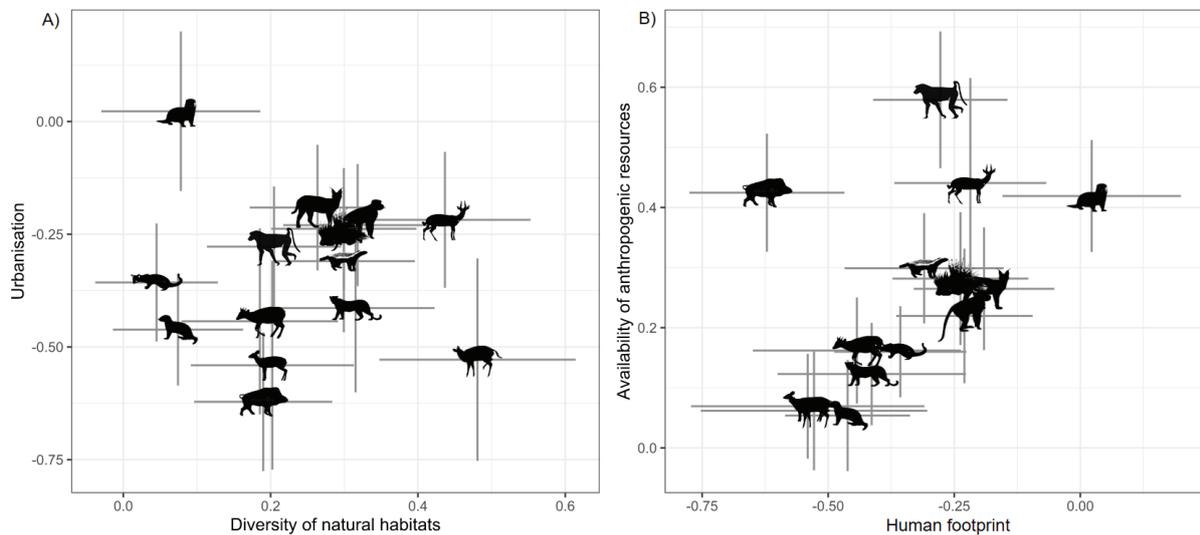
We used the availability of anthropogenic resources and the diversity of natural habitats to apply a 2D representation of the anthropodependence framework proposed by Hulme-Beaman et al. (2016). Species displayed different responses to selected anthropogenic landscape attributes (Figure 3). The blue duiker was strongly related to the presence of natural habitats but not attracted to the availability of anthropogenic resources, which would classify it as an anthropophobic species. Some species, like the baboon and bushpig, were more likely to be found on properties with a high availability of anthropogenic resources, but not a high diversity and integrity of natural habitats, which suggests anthropodependence. The caracal, honey badger, vervet monkey and porcupine did not need many anthropogenic resources or a diversity of natural habitats and could thus be classified as either synanthropic or anthropophilic species. The blue duiker, grysbok, leopard, African clawless otter and common duiker were detected on less than 20% of properties. This low detection rate suggests that they have difficulty persisting in anthropogenic landscapes and could thus be classified as anthropophobic species.



**FIGURE 3** Estimates per species in relation to the diversity of natural habitats and availability of anthropogenic resources. Grey lines represent the standard error of each estimated value. White percentages indicate the proportion of properties where species were recorded. Coloured rings represent, for illustrative purposes, the four species categories of the conceptual framework proposed by Hulme-Beaman et al. (2016). Anthropodependent species consume human food resources and occupy human habitats. Anthropophilic species consume anthropogenic resources but do not reside in human habitats. Synanthropic species may have home ranges that overlap with human-dominated environments but do not consume anthropogenic resources. Anthropophobic species have home ranges that are mainly in natural environments and do not consume human resources.

### 3.6 | Effect of human disturbances

No clear relationship was observed between human footprint and natural environments (Figure 4A). With the exception of the bushpig, species attracted to properties where anthropogenic resources were available tended to be more tolerant to human footprints (Figure 4B).



**FIGURE 4** Estimates for each species in relation to A) the diversity of natural habitats and human footprint and B) the availability of anthropogenic resources and urbanisation. Grey lines represent the standard error of each estimated value.

## 4 | Discussion

The species recorded by more than 10% of respondents were consistent with those occurring in the area based on previous studies and distribution maps (Child et al., 2016; Hanekom & Randall, 2015). Our findings demonstrated that species had idiosyncratic responses to anthropogenic landscapes, and that it was possible to use local ecological knowledge to document the occurrence of wild mammals, particularly the most commonly observed species, in anthropogenic habitats. However, given that most respondents failed to identify tracks or scat, it appears more appropriate to focus on sightings. Successful identification of closely related species, such as mongooses and genets, do not appear possible using the local ecological knowledge of non-specialists. However, grouping species of the same family has allowed us to highlight certain trends.

### 4.1 | Testing the anthropodependence conceptual framework

The results based on the anthropodependence framework assumptions appeared consistent with those obtained by Hulme-Beaman et al. (2016), and seemed even more relevant when combining the effects of disturbance with those of anthropogenic resources and habitat attributes (Sévêque et al., 2020). The classification of baboons as anthropodependent was in agreement with other studies, showing that they have a high ability to adapt to and exploit anthropogenic environments (Hoffman & O’Riain, 2012; Mazue et al., 2022). Because the blue

duiker is a diet and habitat specialist, with highly specific ecological requirements ; it is a good candidate for anthropophobic classification (Hanekom & Wilson, 1991; Venter et al., 2016). Although bushpig find refugia in forests (Hanekom & Randall, 2015), studies have concluded that they might also have the ability to adapt to more urbanised environments (Zungu et al., 2020). Our results suggest that bushpig cannot be classified as anthropodependent but rather anthropophilic. The bushbuck, caracal, honey badger, porcupine and vervet monkey seemed to exhibit an anthropophilic/synanthropic profile, which agreed with the literature (Ehlers Smith et al., 2018; Leighton et al., 2022; Ngcobo et al., 2019; Zungu et al., 2020). The weak association between the presence of genet and mongooses and the availability of resources would suggest that they are synanthropic rather than anthropophilic. However, because respondents struggled to distinguish between the different species of genet and mongooses, these results may be inconclusive. The common duiker, grysbok and leopard appeared to be anthropophobic species, which was consistent with their low observation rates. Although we found no negative relationship with urbanisation and a positive relationship with properties with high anthropogenic resource availability, the low observation rate of otters would position them as anthropophobic. This result may be driven by otters' dependence on artificial dams created by landowners. Overall, some species exhibited a higher tolerance of human disturbances. Additionally, considering human disturbances alongside resource availability and habitat attributes provided a more accurate conceptualisation of species tolerance of or sensitivity to human activity. These findings need to be factored into the conception, design and implementation of conservation initiatives in anthropogenic landscapes.

#### 4.2 | Use of local ecological knowledge

Our study focused on the modified part of the anthropogenic landscape gradient, and we lacked data to control for areas without anthropogenic disturbances, such as the GRNP. However, asking landowners directly about the land-uses, activities and sightings on their properties provided a realistic picture of their characteristics, which is difficult to obtain using other data sources. The low level of importance associated with interference variables (dogs and humans) could be attributed to the fact that most respondents had domestic dogs, and that we focused on human-dominated habitats characterised by human activities. By definition, our focus on anthropogenic landscapes did not provide the information needed to describe anthropophobic species, because these were not expected to occur in human-modified habitats. For instance, the results obtained for the otter cannot be explained and require further investigation to understand the ecology of this species in the GRDM. Nevertheless, the percentage of properties where each species was detected is a good indicator of the ability of mammals to persist in human-dominated landscapes and could serve as a basis for future research. Most respondents were involved in conservation initiatives. Despite our random sampling, we did not receive many responses from persons not interested in conservation (only 2% were not part of a conservation project). Questionnaires are open to human biases (Boakes et al., 2010; White et al., 2005), and inaccuracies may have been recorded because of respondents' difficulty with species identification (Anadón et al., 2010; Jones et al., 2008). Furthermore, because humans are mainly active during the day, the sightings recorded in this survey might be biased in favour of diurnal and crepuscular species (Nyhus et al., 2003), or species that were more easily detected or identified (Pearce & Boyce, 2006). However, Burt et al. (2021) showed that local ecological knowledge can effectively describe the full suite of

species in a mammal community; hence, our data obtained from over 200 observers likely describes the large mammal community in the study area with relative accuracy. Observed species range from charismatic to ordinary, and common to elusive. Because less charismatic and more common species were reported most frequently in this study, we can assume minimal bias associated with species status (Boakes et al., 2010). In addition to its scientific benefits, local ecological knowledge-based research promotes reconnection between people and their surrounding wildlife. In multifunctional landscapes such as those found in the GRDM, it could serve as the first step in designing resilient models for coexistence between humans, their activities and wildlife conservation (Devictor et al., 2010). Considering that South Africa is facing trade-offs between biodiversity protection and poverty reduction, involving people in co-constructed conservation projects can greatly benefit the development of sustainable conservation frameworks (Obura et al., 2021).

### 4.3 | Conservation implications

All species exhibited a positive relationship with the presence and diversity of natural habitats, highlighting the major role that residents can play in protecting wild mammal species by preserving natural vegetation on their properties. Therefore, it is important to establish more private conservation areas, or better preserve existing ones, to provide corridors for ecological connectivity and maintain favourable habitats for wildlife (Brennan et al., 2022). Small fragments of natural habitats in human-dominated landscapes are essential for the persistence of mammals and also contribute to people's quality of life and wellbeing (Obura et al., 2021). Our study also highlighted a lack of local ecological knowledge, despite the relatively high occurrence of various mammals in anthropogenic landscapes. This stresses the need to improve environmental education and engagement with conservation outside protected areas. We documented the negative impact of human footprint on mammals, while demonstrating the possibility of maintaining biodiversity in human-dominated areas. The creation of areas that minimise human disturbances will highly benefit anthropophobic species. We did not observe a direct negative effect of humans or dogs on the species that we studied. This may be because of the method used; because we asked respondents which species they observed on their properties, mammals detected were probably not those frightened by humans or dogs. Furthermore, it is possible that human presence does not play as large a role in habitats already disturbed as in less modified habitats (Nickel et al., 2020). The positive values of the estimates for all species associated with the presence of dogs most likely highlight that people with dogs were more likely to detect species passing through their properties. We only obtained information regarding the presence of domestic dogs; these typically do not hunt wildlife as much as feral dogs, which might further explain why we did not observe any significant associated effect. We did not explore the impact of recreational activities because we focused on private properties. However, it has been shown that recreation has an effect on certain species (Larson et al., 2016). Studies in the GRNP, which facilitates numerous recreational activities, are thus needed to obtain a more complete understanding of mammal responses to multifunctional landscapes.

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## References

- Anadón, J. D., Giménez, A., & Ballestar, R. (2010). Linking local ecological knowledge and habitat modelling to predict absolute species abundance on large scales. *Biodiversity and Conservation*, 19(5), 1443–1454. <https://doi.org/10.1007/s10531-009-9774-4>
- Baard, J., Durrheim, G., Hanekom, N., Hayes, J. S., Kraaij, T., Kruger, N., Ngubeni, N., Randall, R. M., Russell, I. A., Seydack, A. H. W., Smith, K., Van der Vyver, L., & Vermeulen, W. J. (2015). Garden Route National Park—State of knowledge.
- Barton, K. (2022). MuMIn: Multi-Model Inference. R package version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>
- Bennett, N. J., Roth, R., Klain, S. C., Chan, K., Christie, P., Clark, D. A., Cullman, G., Curran, D., Durbin, T. J., Epstein, G., Greenberg, A., Nelson, M. P., Sandlos, J., Stedman, R., Teel, T. L., Thomas, R., Veríssimo, D., & Wyborn, C. (2017). Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation*, 205, 93–108. <https://doi.org/10.1016/j.biocon.2016.10.006>
- Boakes, E. H., McGowan, P. J. K., Fuller, R. A., Chang-qing, D., Clark, N. E., O'Connor, K., & Mace, G. M. (2010). Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLOS Biology*, 8(6), e1000385. <https://doi.org/10.1371/journal.pbio.1000385>
- Bourgeois, R., Guerbois, C., Giva, N., Mugabe, P., Mukamuri, B., Fynn, R., Daré, W., Motsholapheko, M., Nare, L., Delay, E., Ducrot, R., Bucuane, J., Mercandalli, S., Le Page, C., & Caron, A. (2023). Using anticipation to unveil drivers of local livelihoods in Transfrontier Conservation Areas: A call for more environmental justice. *People and Nature*, pan3.10446. <https://doi.org/10.1002/pan3.10446>
- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N., & Kremen, C. (2022). Functional connectivity of the world's protected areas. *Science*, 376(6597), 1101–1104. <https://doi.org/10.1126/science.abl8974>
- Burt, C., Fritz, H., Keith, M., Guerbois, C., & Venter, J. A. (2021). Assessing different methods for measuring mammal diversity in two southern African arid ecosystems. *Mammal Research*, 66(2), 313–326. <https://doi.org/10.1007/s13364-021-00562-x>
- CapeNature. (2017). Western Cape Biodiversity Spatial Plan Handbook.
- Child, F. M., Roxburgh, L., Do Linh San, E., Raimondo, D., & Davies-Mostert, H. T. (2016). The red list of mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa. <[www.ewt.org.za](http://www.ewt.org.za)>.
- Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221–2228. <https://doi.org/10.1016/j.biocon.2010.06.007>
- Cretois, B., Linnell, J. D. C., Van Moorter, B., Kaczensky, P., Nilsen, E. B., Parada, J., & Rød, J. K. (2021). Coexistence of large mammals and humans is possible in Europe's anthropogenic landscapes. *IScience*, 24(9), 103083. <https://doi.org/10.1016/j.isci.2021.103083>
- Crisp, A. G. (2015). Development role players' knowledge of ecological infrastructure in Eden district, South Africa.

[http://vital.seals.ac.za:8080/vital/access/manager/Repository/vital:26424?site\\_name=GlobalView](http://vital.seals.ac.za:8080/vital/access/manager/Repository/vital:26424?site_name=GlobalView)

Devictor, V., Whittaker, R. J., & Beltrame, C. (2010). Beyond scarcity: Citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions*, 16(3), 354–362. <https://doi.org/10.1111/j.1472-4642.2009.00615.x>

Diaz, S. (2019). Pervasive human-driven decline of life on Earth points to the need for profound change. *Science*, 331(6015), 341–346. <https://doi.org/10.1126/science.1194732>

Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Phillips, T., & Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10(6), 291–297. <https://doi.org/10.1890/110236>

Dray, S., & Dufour, A. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, 22(4), 1–20. <https://doi.org/10.18637/jss.v022.i04>

Drouilly, M., Natrass, N., & O’Riain, M. J. (2018). Dietary niche relationships among predators on farmland and a protected area: Diet of Predators on Contrasting Land Uses. *The Journal of Wildlife Management*, 82(3), 507–518. <https://doi.org/10.1002/jwmg.21407>

Ehlers Smith, Y. C., Ehlers Smith, D. A., Ramesh, T., & Downs, C. T. (2018). Forest habitats in a mixed urban-agriculture mosaic landscape: Patterns of mammal occupancy. *Landscape Ecology*, 33(1), 59–76. <https://doi.org/10.1007/s10980-017-0580-1>

Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, 118(17), e2023483118. <https://doi.org/10.1073/pnas.2023483118>

Fleming, P. A., & Bateman, P. W. (2018). Novel predation opportunities in anthropogenic landscapes. *Animal Behaviour*, 138, 145–155. <https://doi.org/10.1016/j.anbehav.2018.02.011>

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression*, Third Edition. Thousand Oaks CA: Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>

Gatiso, T. T., Kulik, L., Bachmann, M., Bonn, A., Bösch, L., Eirdosh, D., Freytag, A., Hanisch, S., Heurich, M., Sop, T., Wesche, K., Winter, M., & Köhl, H. S. (2022). Effectiveness of protected areas influenced by socio-economic context. *Nature Sustainability*, 5, 861–868. <https://doi.org/10.1038/s41893-022-00932-6>

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360(6394), 1232–1235. <https://doi.org/10.1126/science.aar7121>

Geldmann, J., Manica, A., Burgess, N. D., Coad, L., & Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proceedings of the National Academy of Sciences*, 116(46), 23209–23215. <https://doi.org/10.1073/pnas.1908221116>

Hanekom, N., & Randall, R. M. (2015). Assessments of occurrence and distribution of mammals in forests of the Garden Route National Park based on camera trapping. *Koedoe*, 57(1), a1257. <https://doi.org/10.4102/koedoe.v57i1.1257>

Hanekom, N., & Wilson, V. (1991). Blue duiker *Philantomba monticola* densities in the Tsitsikamma National Park and probable factors limiting these populations. *Koedoe*, 34(2), Article 2.

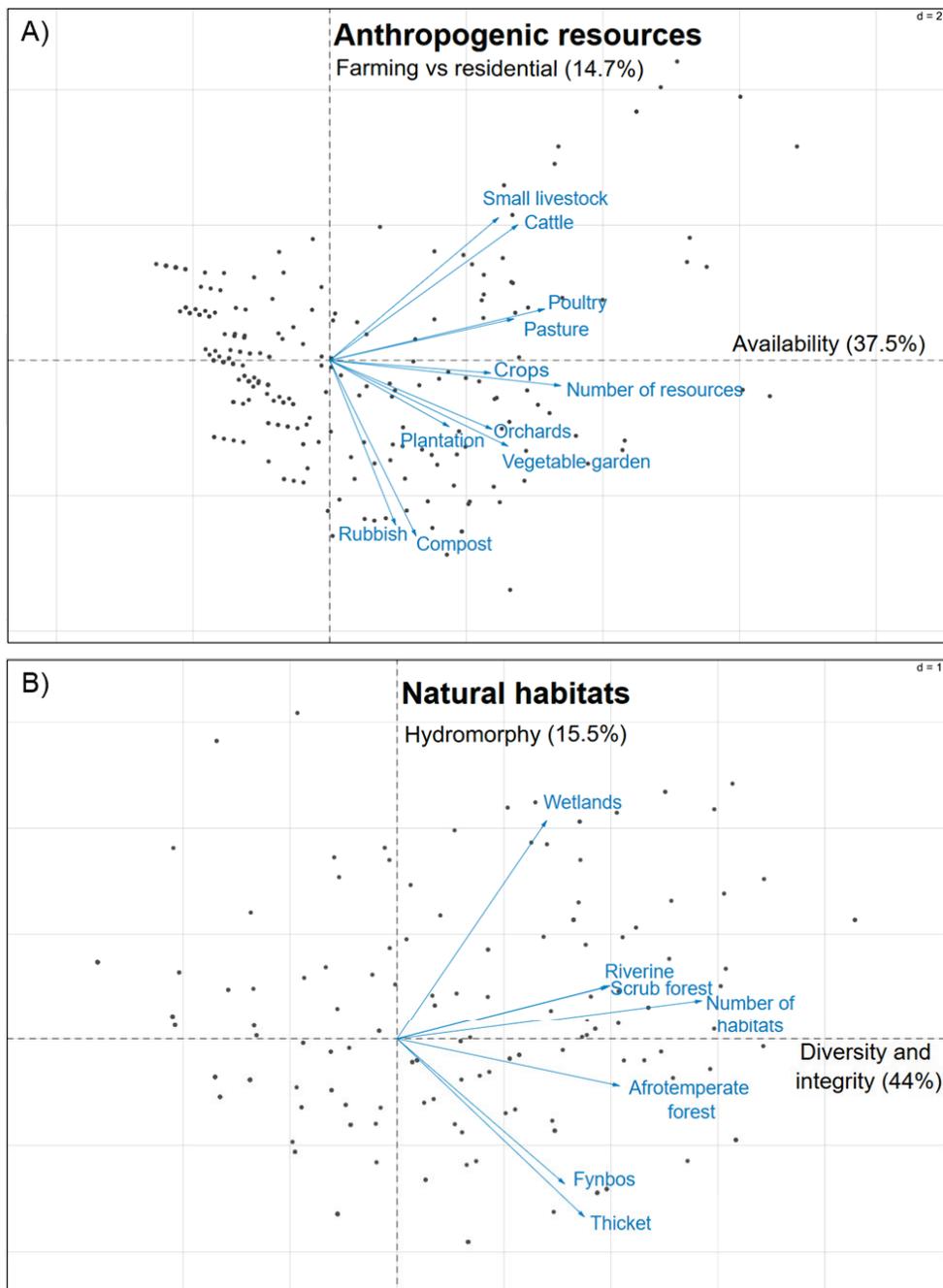
Hoffman, T. S., & O’Riain, M. J. (2012). Landscape requirements of a primate population in a human-dominated environment. *Frontiers in Zoology*, 9(1), 1. <https://doi.org/10.1186/1742-9994-9-1>

- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, 31(8), 633–645. <https://doi.org/10.1016/j.tree.2016.05.001>
- Jones, J. P. G., Andriamarivololona, M. M., Hockley, N., Gibbons, J. M., & Milner-Gulland, E. J. (2008). Testing the use of interviews as a tool for monitoring trends in the harvesting of wild species. *Journal of Applied Ecology*, 45(4), 1205–1212. <https://doi.org/10.1111/j.1365-2664.2008.01487.x>
- Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2020). Global Human Modification of Terrestrial Systems. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/edbc-3z60>
- Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review. *PLOS ONE*, 11(12), e0167259. <https://doi.org/10.1371/journal.pone.0167259>
- Leighton, G. R. M., Bishop, J. M., Merondun, J., Winterton, D. J., O’Riain, M. J., & Serieys, L. E. K. (2022). Hiding in plain sight: Risk mitigation by a cryptic carnivore foraging at the urban edge. *Animal Conservation*, 25(2), 244–258. <https://doi.org/10.1111/acv.12732>
- Mazue, F., Guerbois, C., Fritz, H., Rebut, N., & Petit, O. (2022). Less bins, less baboons: Reducing access to anthropogenic food effectively decreases the urban foraging behavior of a troop of chacma baboons (*Papio hamadryas ursinus*) in a peri-urban area. *Primates*, 64, 91–103. <https://doi.org/10.1007/s10329-022-01032-x>
- Natrass, N., & O’Riain, M. J. (2020). Contested natures: Conflict over caracals and cats in Cape Town, South Africa. *Journal of Urban Ecology*, 6(1), juaa019. <https://doi.org/10.1093/jue/juaa019>
- Ngcobo, S. P., Wilson, A.-L., & Downs, C. T. (2019). Habitat selection of Cape porcupines in a farmland-suburban context in KwaZulu-Natal, South Africa. *Mammalian Biology*, 98, 111–118. <https://doi.org/10.1016/j.mambio.2019.08.004>
- Nickel, B. A., Suraci, J. P., Allen, M. L., & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, 241, 108383. <https://doi.org/10.1016/j.biocon.2019.108383>
- Nyhus, P. J., Sumianto, & Tilson, R. (2003). Wildlife knowledge among migrants in southern Sumatra, Indonesia: Implications for conservation. *Environmental Conservation*, 30(2), 192–199. <https://doi.org/10.1017/S0376892903000183>
- Obura, D. O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoily, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M., & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, 373(6556), 746–748. <https://doi.org/10.1126/science.abh2234>
- Pearce, J. L., & Boyce, M. S. (2006). Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, 43(3), 405–412. <https://doi.org/10.1111/j.1365-2664.2005.01112.x>
- Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10(1), 439–446. <https://doi.org/10.32614/RJ-2018-009>
- Pédarros, É., Coetzee, T., Fritz, H., & Guerbois, C. (2020). Rallying citizen knowledge to assess wildlife occurrence and habitat suitability in anthropogenic landscapes. *Biological Conservation*, 242, 108407. <https://doi.org/10.1016/j.biocon.2020.108407>
- Pool-Stanvliet, R., & Coetzer, K. (2020). The scientific value of UNESCO biosphere reserves. *South African Journal of Science*, 116(1/2). <https://doi.org/10.17159/sajs.2020/7432>
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

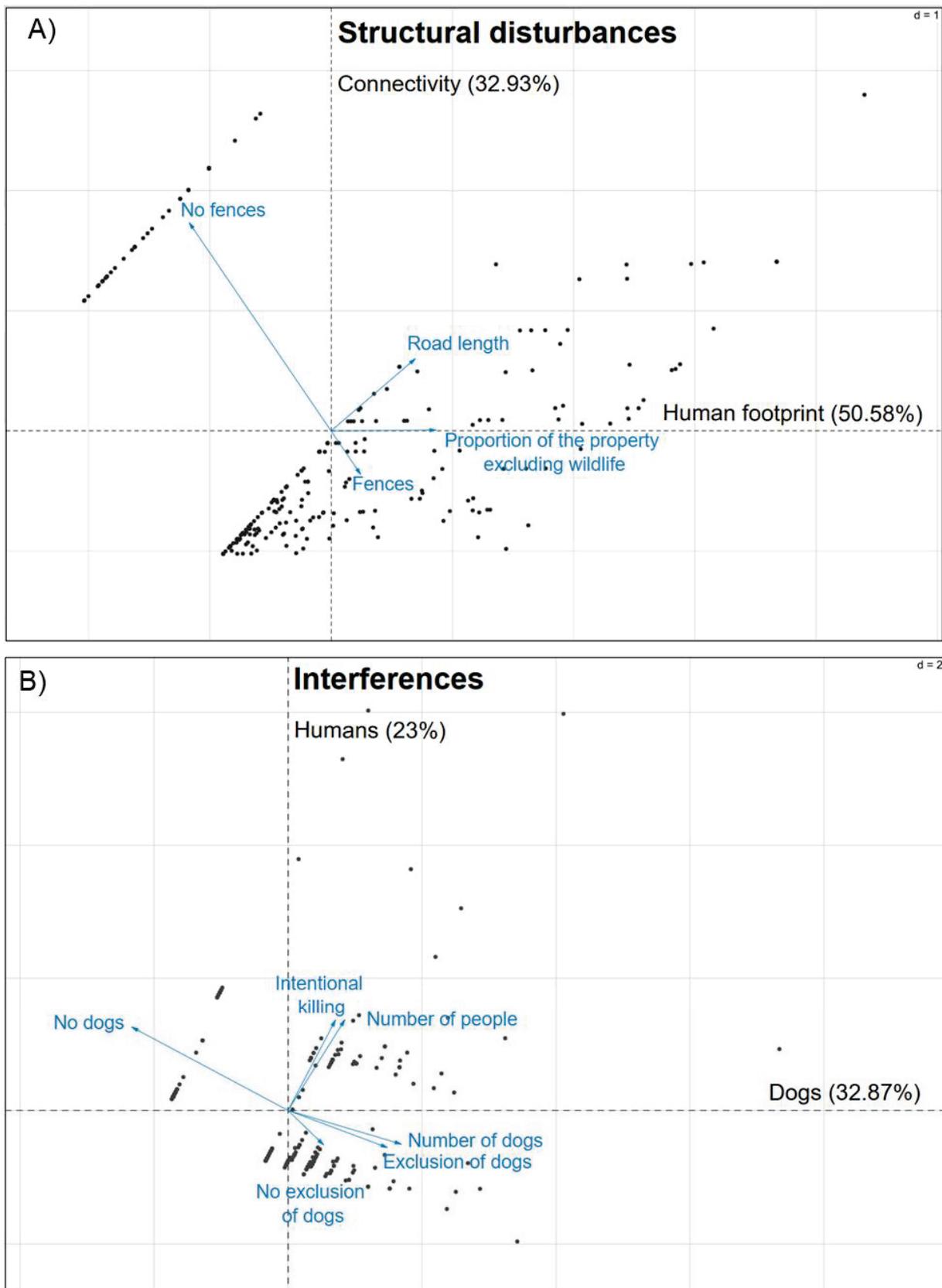
- Rosenzweig, M. L. (2003). Reconciliation ecology and the future of species diversity. *Oryx*, 37(2), 194–205. <https://doi.org/10.1017/S0030605303000371>
- SANParks. (2020). Garden Route National Park: Park Management Plan For the period 2020—2029. Pretoria: Department of Environment, Forestry and Fisheries.
- Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., & Ancillotto, L. (2019). One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology Letters*, 22(2), 365–376. <https://doi.org/10.1111/ele.13199>
- Sebastián-González, E., Barbosa, J. M., Pérez-García, J. M., Morales-Reyes, Z., Botella, F., Olea, P. P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J. A., Cortés-Avizanda, A., Selva, N., Lambertucci, S. A., Bhattacharjee, A., Brewer, A., Anadón, J. D., Abernethy, E., Rhodes Jr, O. E., ... Sánchez-Zapata, J. A. (2019). Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology*, 25(9), 3005–3017. <https://doi.org/10.1111/gcb.14708>
- Sévêque, A., Gentle, L. K., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95(6), 1689–1705. <https://doi.org/10.1111/brv.12635>
- Swanson, A., Kosmala, M., Lintott, C., Simpson, R., Smith, A., & Packer, C. (2015). Snapshot Serengeti, high-frequency annotated camera trap images of 40 mammalian species in an African savanna. *Scientific Data*, 2(150026), Article 1. <https://doi.org/10.1038/sdata.2015.26>
- Venter, J., Seydack, A., Ehlers Smith, Y., Uys, R., & Child, M. F. (2016). A conservation assessment of *Philantomba monticola*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa. 9.
- Weinzettel, J., Vačkář, D., & Medková, H. (2018). Human footprint in biodiversity hotspots. *Frontiers in Ecology and the Environment*, 16(8), 447–452. <https://doi.org/10.1002/fee.1825>
- Western Cape Government. (2019). Socio-economic profile: Garden Route District Municipality. <https://www.westerncape.gov.za/provincial-treasury/files/atoms/files/SEP-LG%202021%20-%20Garden%20Route%20District%20Municipality.pdf>
- White, P. C. L., Jennings, N. V., Renwick, A. R., & Barker, N. H. L. (2005). Questionnaires in ecology: A review of past use and recommendations for best practice. *Journal of Applied Ecology*, 42(3), 421–430. <https://doi.org/10.1111/j.1365-2664.2005.01032.x>
- Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.
- Williams, B. A., Venter, O., Allan, J. R., Atkinson, S. C., Rehbein, J. A., Ward, M., Di Marco, M., Grantham, H. S., Ervin, J., Goetz, S. J., Hansen, A. J., Jantz, P., Pillay, R., Rodríguez-Buriticá, S., Supples, C., Virnig, A. L. S., & Watson, J. E. M. (2020). Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems. *One Earth*, 3(3), 371–382. <https://doi.org/10.1016/j.oneear.2020.08.009>
- Young, B. E., Dodge, N., Hunt, P. D., Ormes, M., Schlesinger, M. D., & Shaw, H. Y. (2019). Using citizen science data to support conservation in environmental regulatory contexts. *Biological Conservation*, 237, 57–62. <https://doi.org/10.1016/j.biocon.2019.06.016>
- Zungu, M. M., Maseko, M. S. T., Kalle, R., Ramesh, T., & Downs, C. T. (2020). Factors affecting the occupancy of forest mammals in an urban-forest mosaic in EThekweni Municipality, Durban, South Africa. *Urban Forestry & Urban Greening*, 48, 126562. <https://doi.org/10.1016/j.ufug.2019.126562>

## Supplementary material for the manuscript 3: A local ecological knowledge-based assessment of anthropodependence for large mammals in anthropogenic landscapes

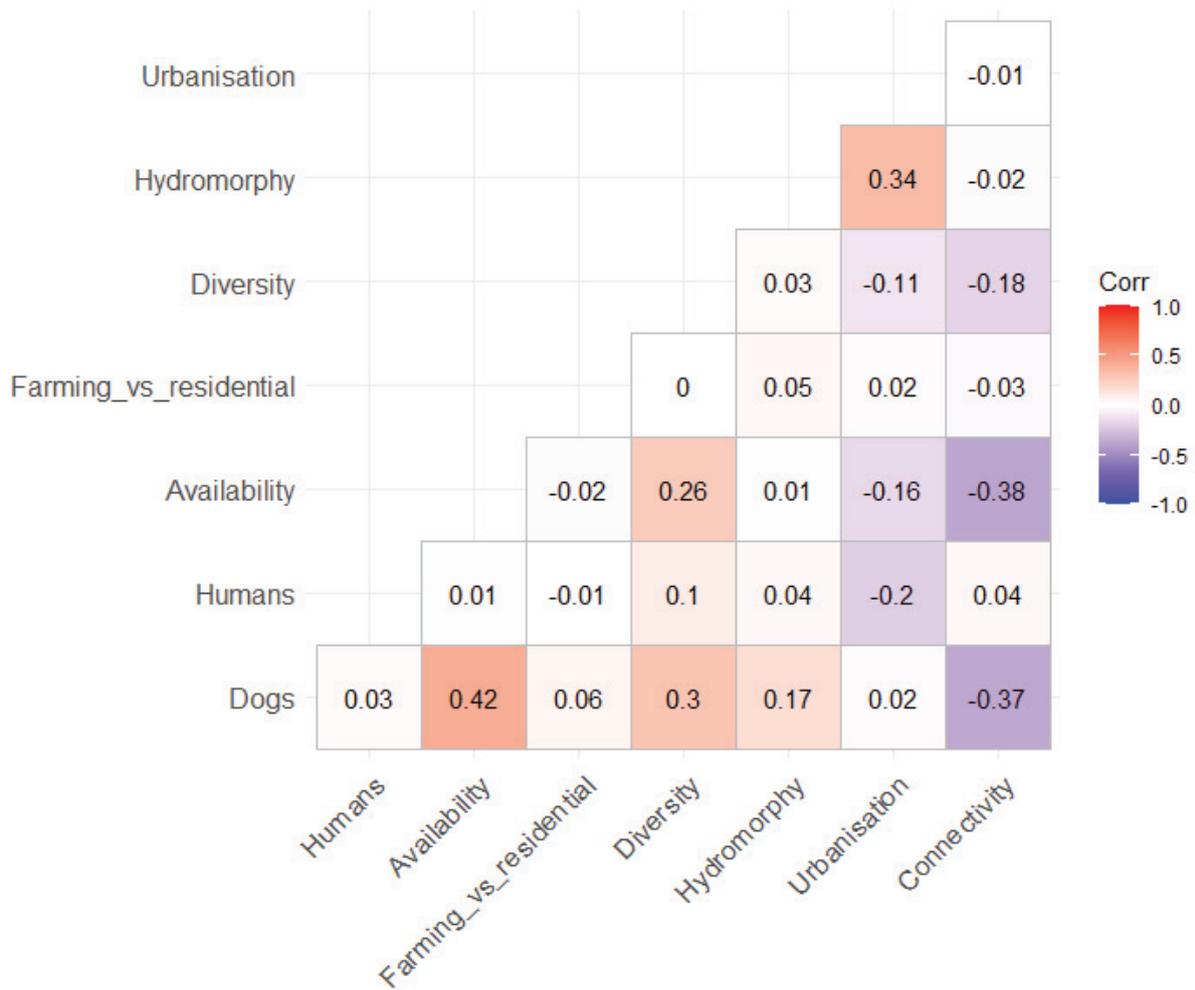
### Figures



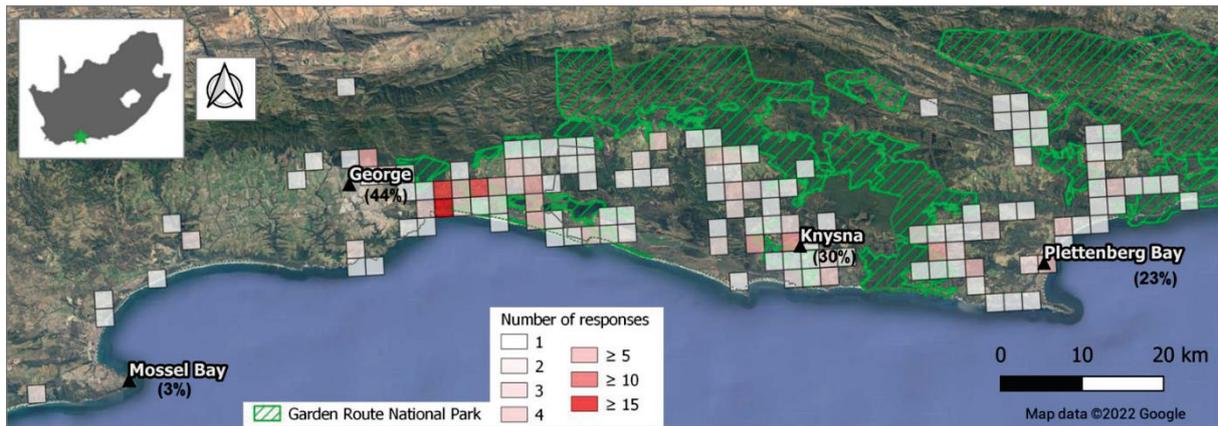
**FIGURE S1** Results of the Principal Component Analyses (PCA) to describe A) anthropogenic resources, and B) natural habitats among the surveyed properties.



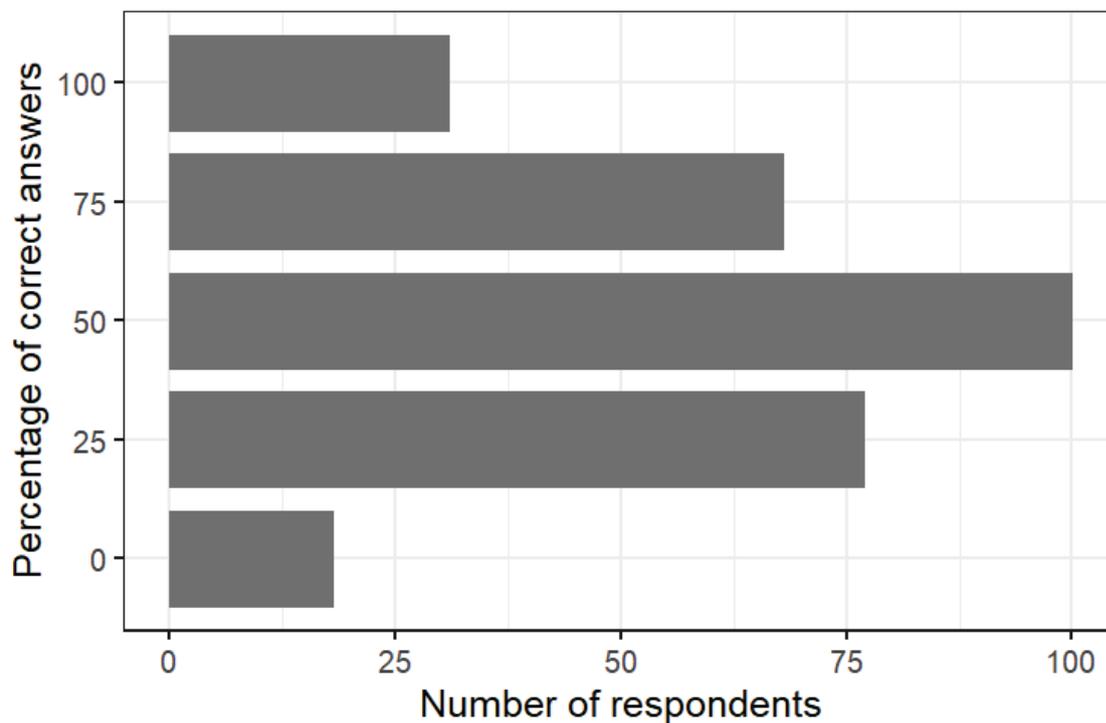
**FIGURE S2** Results of the multivariate analysis with mixed quantitative variables and factors (Hill and Smith analysis) describing A) structural disturbances and B) interferences among the surveyed properties.



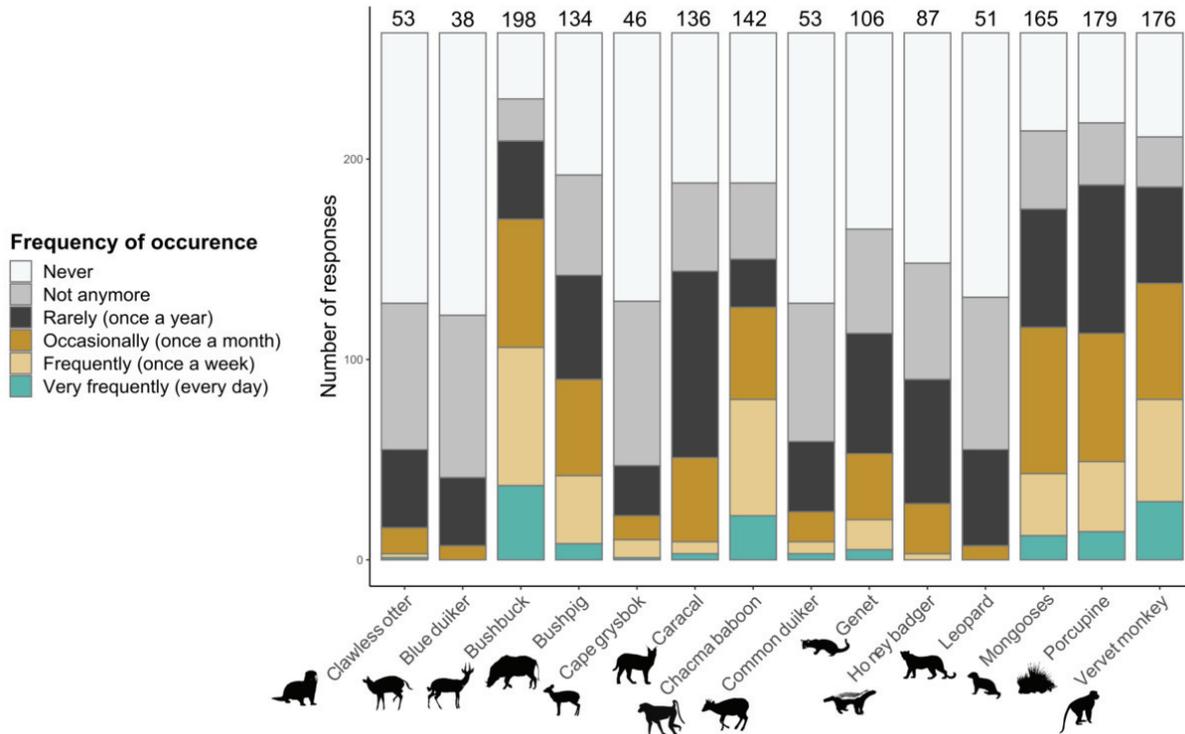
**FIGURE S3** Correlation between the variables obtained from the multivariate analyses to describe the 4 different gradients used. There is no correlation, so all variables were used in the following models.



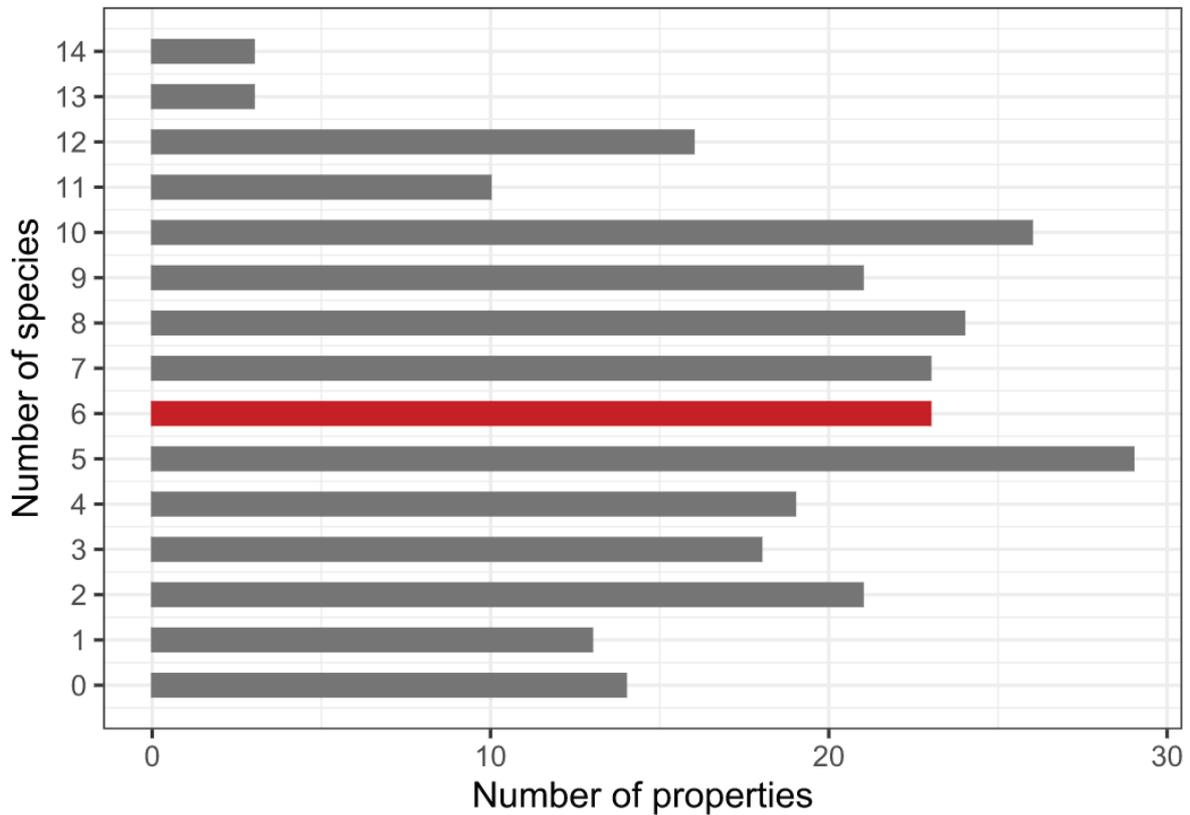
**FIGURE S4** Study site in the Garden Route, South Africa. The cells represent the survey grid, and are coloured by the number of responses. The borders of the Garden Route National Park are represented in green.



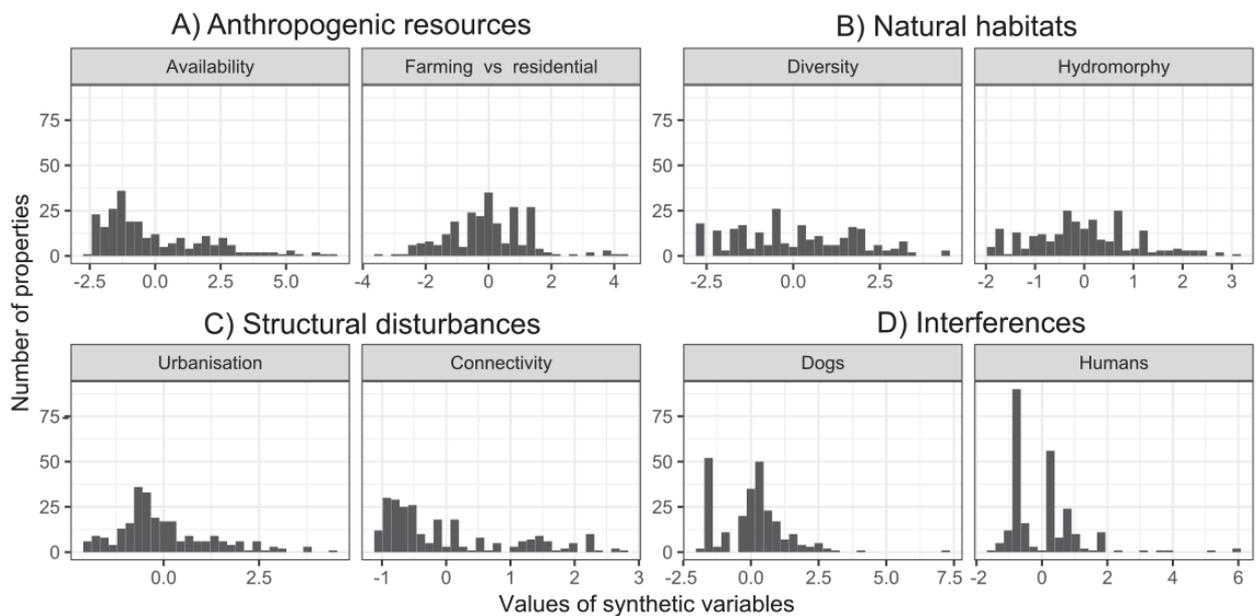
**FIGURE S5** Histogram representing the results of respondent to the naturalist knowledge questions.



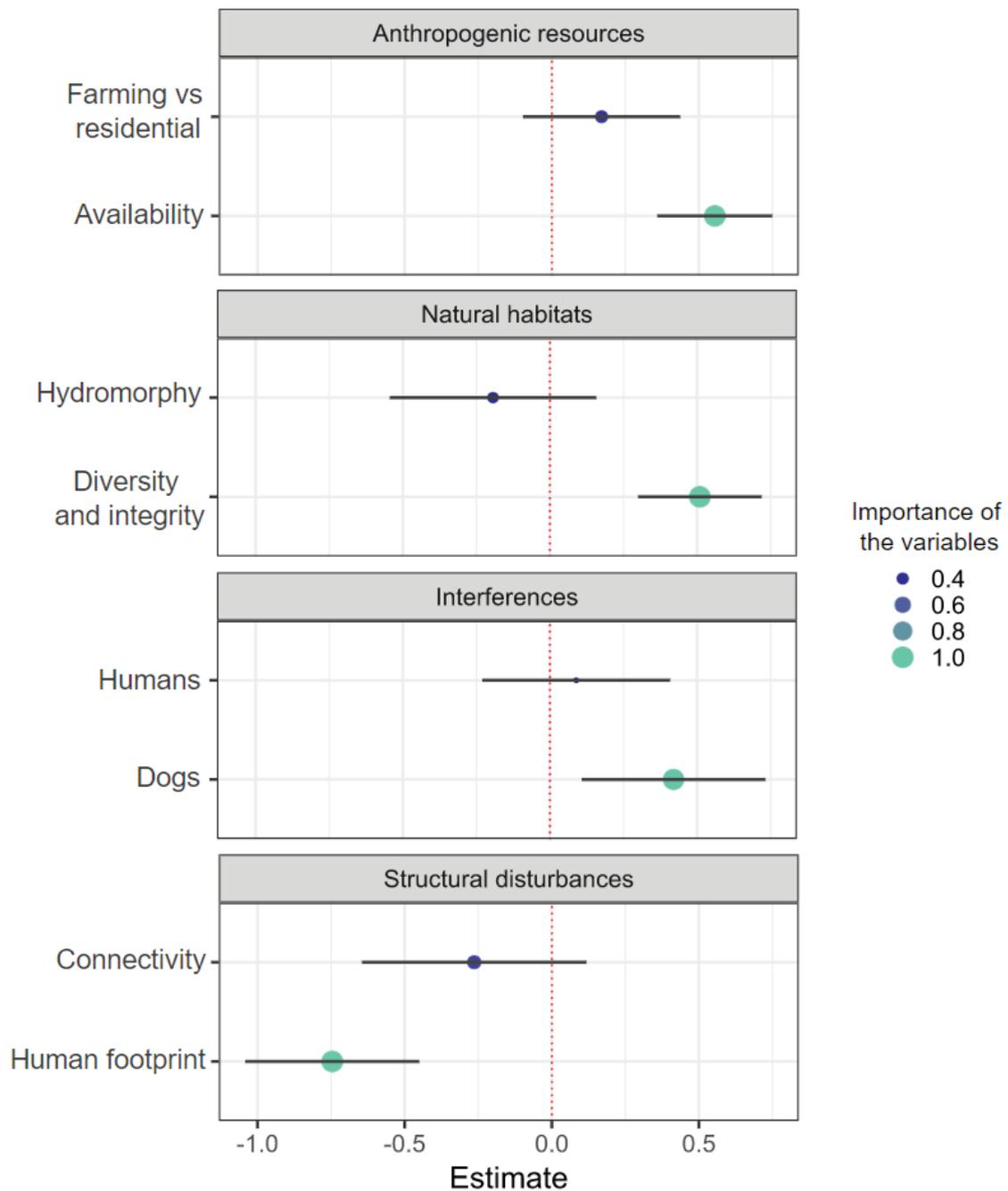
**FIGURE S6** Number of responses for each of the 14 most cited species and their frequency of occurrence on the properties. Light grey for species that were not cited, grey for species that are no longer present on the property, black for those that are rarely present, dark yellow for occasional presence, yellow for species that are frequently present and blue when they are very frequently present.



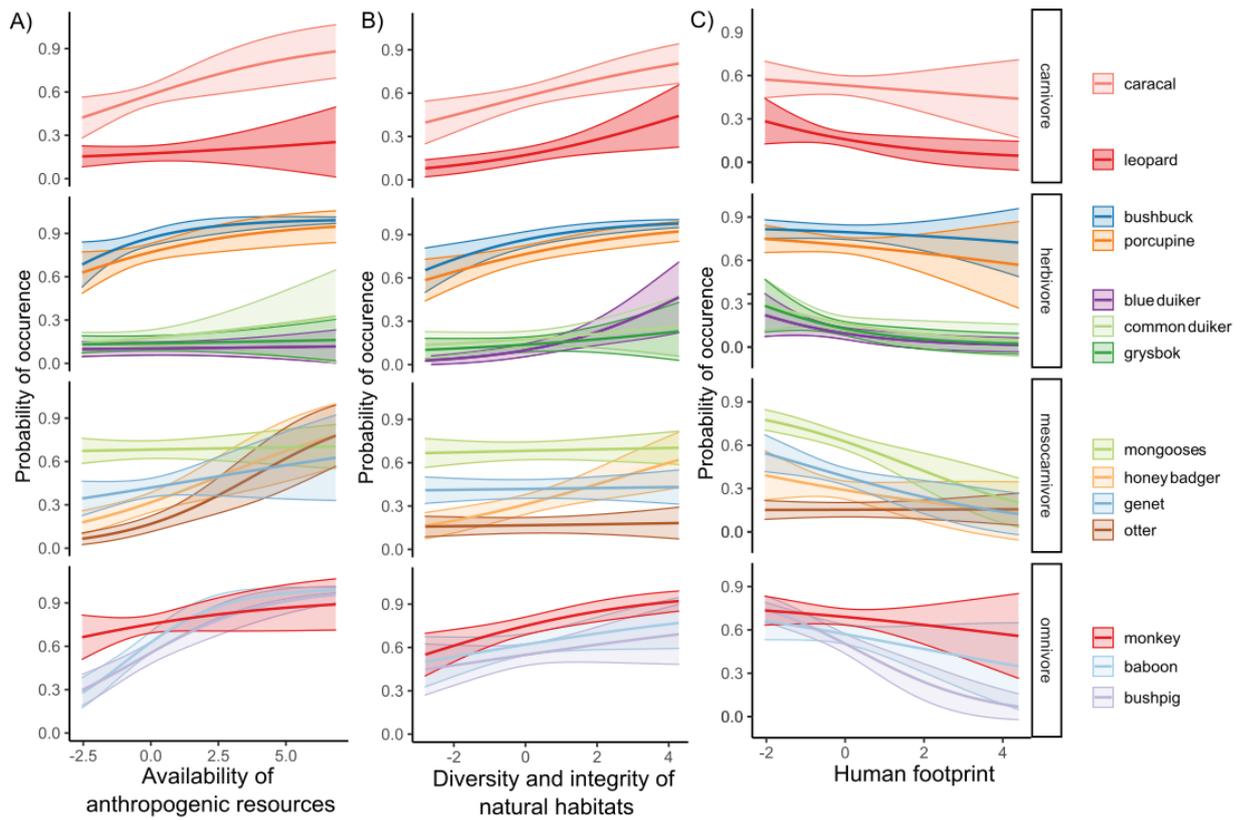
**FIGURE S7** Number of species detected per property. On average, 6.3 species were detected.



**FIGURE S8** Histograms of the variables obtained from the multivariate analyses to describe the four different gradients used: A) anthropogenic resources; B) natural habitats; C) structural disturbances; D) interferences.



**FIGURE S9** Representation of the estimates (gradient of blue) for the number of species per properties of the two first axes kept for each gradient (synthetic variables). The size and color of the points depend on the value of the sum of weight. The largest points in blue/green represent the most important variables for a species. The black lines represent the 95% confidence interval for each estimated value ('confint' function, 'stats' R package). The red lines highlight the position of 0 on the x-axis. If the confidence interval of a variable does not include 0, it means that the variable is significant. The further away from 0, the more important the variable is. To the right of the lines, species occurrence has a positive relationship to the variable.



**FIGURE S10** Representation of predicted probability of occurrence according to A) the availability of anthropogenic resources and B) the diversity of natural habitats and C) the human footprint gradient, coloured by species.

## Tables

**TABLE S1** Description of the questions used for species presence and for constructing gradients of anthropogenic resources, natural habitats, structural disturbances and interferences.

Objectives	Questions	Type of question	Name of the variable	Data used
<b>Species occurrence</b>	The following species are known to be present in the Garden Route National Park. Please specify how regularly you have observed the presence of the following species on your property, over the past 3 years: (leave blank if you do not know)	Multiple choices	Presence/absence of a species	<u>Binary</u> : 0 = no answer or not anymore; 1 = very frequently, frequently, occasionally or rarely
<b>Anthropogenic resources</b>	What different land use can be found on your property?	Multiple choices	<u>Presence</u> : pasture, crops, orchards, plantation, vegetable garden	<u>Binary</u> : 0 = absent; 1 = present
	Do you compost your biodegradable waste?	Multiple choices	Compost	<u>Numeric</u> : 0 = no; 1 = yes ; 2= accessible to wildlife
	Do wild mammal species have access to your rubbish bags?	Multiple choices	Rubbish	<u>Numeric</u> : 0 = no; 1 = yes ; 2= accessible to wildlife
	What domestic animals do you keep on your property? (Leave blank if not applicable)	Multiple choices	<u>Presence</u> : small livestock, cattle, poultry	<u>Binary</u> : 0 = absent; 1 = present
	If you experienced any wild mammal related damage, injuries or loss on your property, what was affected? Leave blank if you have not experienced any damage.	Multiple choices	<u>Availability</u> : pasture, crops, orchards, plantation, vegetable garden, small livestock, cattle, poultry	<u>Numeric</u> : 2 = when people said they had damage on a modified habitat or domestic animal
Sum of the presence of the previous questions	Calculated from previous variables	Number of resource	<u>Numeric</u> : 0 to 15	
<b>Natural habitats</b>	What different habitats/vegetation can be found on your property and in which state?	Multiple choices	<u>Presence and state</u> : Wetlands, riverine, scrub forest, Afrotropical forest, thicket, fynbos	<u>Numeric</u> : 0 = absent, 1 = present but disturbed or in rehabilitation; 2 = present and natural
	Sum of the presence of the previous question	Calculated from previous variables	Number of habitat	<u>Numeric</u> : 0 to 6
<b>Structural disturbance</b>	Is your property fenced?	Multiple choices	Fences	<u>Binary</u> : 0 = no; 1 = yes
	Which proportion of your property totally excludes wild mammal species?	Open	Proportion excluding wildlife	<u>Numeric</u> : 0 to 100%
	Length of roads in a 2,23*2,23 km cell	Calculated from a shapefile	Road length	<u>Numeric</u> : 0 to 56989 meters
<b>Interference</b>	Have any of these activities occurred on your property in the last 3 years?	Multiple choices	Intentional killing	<u>Binary</u> : 1 = Snaring, hunting, dog hunting or poisoning; 0 = when nothing happened
	Could you specify their number and breeds? If you don't have a dog, you can skip the following 4 questions.	Open	Number of dogs	<u>Numeric</u> : 1 to 20
	Which proportion of your property totally excludes your dogs?	Open	Exclusion dogs	<u>Numeric</u> , transformed to <u>categorical variables</u> : No dogs, exclusion dogs, no exclusion dogs
	On average, how many people are on your property every day?	Open	Number of people	<u>Numeric</u> : 1 to 150

**TABLE S2** Percentage of methods of detection used by the respondents to detect a species on their properties. We asked the survey participants how they knew the species were on their property. They had 11 possibilities which are listed in the columns below. On the properties where the species were present, we calculated the proportion of the detection method used. We have bolded the most used method for all species. The main method of detection was sightings.

Species	Sightings (%)	Tracks (%)	Scats (%)	Hair (%)	Sounds (%)	Feeding signs (%)	Burrows (%)	Species carcasses (%)	Camera traps (%)	Someone told you (%)	Other signs (%)
Bushbuck	<b>92</b>	43	32	4	19	17	1	5	22	3	0
Porcupine	<b>63</b>	25	19	16	8	41	12	3	21	4	13
Vervet monkey	<b>93</b>	6	8	0	43	14	0	1	6	2	1
Mongoose	<b>44</b>	2	1	0	0	3	0	0	3	1	1
Chacma baboon	<b>94</b>	29	42	5	58	36	0	3	13	3	1
Caracal	<b>71</b>	23	17	2	3	15	0	3	20	11	2
Bushpig	<b>49</b>	43	44	2	17	42	8	1	25	5	2
Genet	<b>51</b>	4	5	0	0	13	0	1	12	5	2
Honey badger	<b>61</b>	21	4	2	7	27	2	0	29	10	7
Common duiker	<b>51</b>	24	7	2	3	3	3	0	10	5	0
African clawless otter	<b>55</b>	24	25	0	2	20	2	5	11	11	7
Leopard	<b>33</b>	<b>33</b>	13	2	18	11	0	0	31	27	0
Cape grysbok	<b>62</b>	17	11	0	2	6	0	2	26	4	2
Blue duiker	<b>39</b>	22	12	2	0	0	5	2	24	7	2

**TABLE S3** Summary table of the 25 cited species sorted by number of citations.

English name	Latin name	Number of citations
<b>Bushbuck</b>	<i>Tragelaphus scriptus</i>	198
<b>Porcupine</b>	<i>Hystrix africaeaustralis</i>	179
<b>Vervet monkey</b>	<i>Chlorocebus pygerythrus</i>	176
<b>Mongoose</b>		165
<b>Baboon</b>	<i>Papio ursinus</i>	142
<b>Caracal</b>	<i>Caracal caracal</i>	136
<b>Bushpig</b>	<i>Potamochoerus larvatus</i>	134
<b>Genet</b>		106
<b>Honey badger</b>	<i>Mellivora capensis</i>	87
<b>Cape grey mongoose</b>	<i>Galerella pulverulenta</i>	86
<b>Cape clawless otter</b>	<i>Aonyx capensis</i>	53
<b>Common duiker</b>	<i>Sylvicapra grimmia</i>	53
<b>Large grey mongoose</b>	<i>Herpestes ichneumon</i>	52
<b>Leopard</b>	<i>Panthera pardus</i>	51
<b>Small-spotted genet</b>	<i>Genetta genetta</i>	48
<b>Grysbok</b>	<i>Raphicerus melanotis</i>	46
<b>Large-spotted genet</b>	<i>Genetta tigrina</i>	39
<b>Blue duiker</b>	<i>Philantomba monticola</i>	38
<b>Water mongoose</b>	<i>Atilax paludinosus</i>	29
<b>African wildcat</b>	<i>Felis silvestris</i>	18
<b>Grey rhebuck</b>	<i>Pelea capreolus</i>	15
<b>Steenbok</b>	<i>Raphicerus campestris</i>	7
<b>Aardvark</b>	<i>Orycteropus afer</i>	7
<b>Striped polecat</b>	<i>Ictonyx striatus</i>	5
<b>Striped weasel</b>	<i>Poecilogale albinucha</i>	5
<b>Elephant</b>	<i>Loxodonta africana</i>	3

**TABLE S4** Results of the model averaging explaining the number of species detected per property

Variables	Estimate	Standard Error	P-value	Minimum Confidence Interval	Maximum Confidence Interval	Importance of the variable
<b>(Intercept)</b>	6.29	0.171	<0.05	5.96	6.63	NA
<b>Availability</b>	0.55	0.10	<0.05	0.36	0.75	1.00
<b>Farming vs residential</b>	0.17	0.14	2.1E-01	-0.10	0.44	0.43
<b>Diversity</b>	0.51	0.11	2.0E-06	0.30	0.72	1.00
<b>Hydromorphy</b>	-0.19	0.18	2.8E-01	-0.54	0.16	0.38
<b>Urbanisation</b>	-0.75	0.15	8.0E-07	-1.04	-0.45	1.00
<b>Connectivity</b>	-0.26	0.19	1.8E-01	-0.65	0.12	0.48
<b>Dogs</b>	0.42	0.16	8.4E-03	0.11	0.73	0.97
<b>Humans</b>	0.09	0.16	5.8E-01	-0.23	0.41	0.28

**TABLE S4** Results of the model averaging explaining the presence/absence of species, classified by diet.

## A) Omnivores

Species	Variables	Estimate	Standard Error	P-value	Minimum Confidence Interval	Maximum Confidence Interval	Importance of the variable
<b>Baboon</b>	(Intercept)	0.51	0.16	2.2E-03	0.18	0.83	NA
	Availability	0.58	0.11	4.0E-07	0.36	0.80	1.00
	Farming vs residential	0.05	0.15	7.3E-01	-0.25	0.35	0.26
	Diversity	0.20	0.09	2.5E-02	0.03	0.38	0.84
	Hydromorphy	0.23	0.16	1.5E-01	-0.08	0.53	0.51
	Urbanisation	-0.28	0.13	3.8E-02	-0.54	-0.02	0.82
	Connectivity	-0.06	0.16	6.8E-01	-0.37	0.24	0.26
	Dogs	-0.03	0.14	8.3E-01	-0.30	0.24	0.25
	Humans	0.01	0.14	9.2E-01	-0.26	0.29	0.25
<b>Bushpig</b>	(Intercept)	0.20	0.16	2.1E-01	-0.11	0.50	NA
	Availability	0.42	0.10	1.7E-05	0.23	0.62	1.00
	Farming vs residential	-0.20	0.13	1.2E-01	-0.46	0.05	0.54
	Diversity	0.19	0.09	4.4E-02	0.01	0.37	0.77
	Hydromorphy	-0.26	0.16	1.0E-01	-0.57	0.05	0.59
	Urbanisation	-0.62	0.15	5.8E-05	-0.92	-0.32	1.00
	Connectivity	0.01	0.16	9.6E-01	-0.31	0.33	0.23
	Dogs	0.10	0.14	4.9E-01	-0.18	0.37	0.29
	Humans	0.14	0.14	3.2E-01	-0.14	0.42	0.35
<b>Vervet monkey</b>	(Intercept)	1.09	0.17	0.0E+00	0.76	1.42	NA
	Availability	0.22	0.11	5.1E-02	0.00	0.44	0.77
	Farming vs residential	-0.06	0.14	6.8E-01	-0.33	0.21	0.27
	Diversity	0.32	0.10	1.7E-03	0.12	0.52	1.00
	Hydromorphy	0.24	0.17	1.7E-01	-0.10	0.58	0.49
	Urbanisation	-0.23	0.14	9.1E-02	-0.50	0.04	0.63
	Connectivity	-0.27	0.16	9.8E-02	-0.60	0.05	0.60
	Dogs	0.29	0.17	8.5E-02	-0.04	0.62	0.65
	Humans	0.17	0.18	3.4E-01	-0.18	0.53	0.36

## B) Carnivores

Species	Variables	Estimate	Standard Error	P-value	Minimum Confidence Interval	Maximum Confidence Interval	Importance of the variable
<b>Caracal</b>	(Intercept)	0.30	0.16	5.6E-02	-0.01	0.60	NA
	Availability	0.26	0.10	9.8E-03	0.06	0.47	0.96
	Farming vs residential	0.15	0.14	2.9E-01	-0.13	0.43	0.37
	Diversity	0.26	0.09	4.4E-03	0.08	0.44	0.99
	Hydromorphy	-0.33	0.15	3.3E-02	-0.63	-0.03	0.79
	Urbanisation	-0.19	0.14	1.7E-01	-0.47	0.08	0.49
	Connectivity	-0.16	0.16	3.4E-01	-0.48	0.16	0.36
	Dogs	0.53	0.16	1.1E-03	0.21	0.84	1.00
	Humans	0.24	0.16	1.3E-01	-0.07	0.55	0.56
<b>Leopard</b>	(Intercept)	-1.58	0.19	0.0E+00	-1.96	-1.20	NA
	Availability	0.12	0.09	1.5E-01	-0.04	0.29	0.51
	Farming vs residential	0.03	0.12	8.1E-01	-0.22	0.28	0.25
	Diversity	0.32	0.11	3.4E-03	0.10	0.53	0.99
	Hydromorphy	-0.01	0.17	9.6E-01	-0.35	0.33	0.26
	Urbanisation	-0.41	0.19	2.7E-02	-0.78	-0.05	0.89
	Connectivity	-0.29	0.20	1.6E-01	-0.68	0.11	0.51
	Dogs	0.19	0.15	2.1E-01	-0.10	0.47	0.46
	Humans	-0.18	0.16	2.9E-01	-0.50	0.15	0.38

## C) Herbivores

Species	Variables	Estimate	Standard Error	P-value	Minimum Confidence Interval	Maximum Confidence Interval	Importance of the variable
Blue duiker	(Intercept)	-2.20	0.26	0.0E+00	-2.71	-1.70	NA
	Availability	0.06	0.10	5.3E-01	-0.13	0.26	0.31
	Farming vs residential	0.31	0.15	3.8E-02	0.02	0.60	0.79
	Diversity	0.48	0.13	3.3E-04	0.22	0.74	1.00
	Hydromorphy	-0.15	0.20	4.7E-01	-0.54	0.25	0.31
	Urbanisation	-0.53	0.22	1.9E-02	-0.97	-0.09	0.94
	Connectivity	0.17	0.22	4.4E-01	-0.27	0.61	0.32
	Dogs	0.34	0.17	4.4E-02	0.01	0.68	0.79
	Humans	-0.04	0.17	8.3E-01	-0.36	0.29	0.25
Bushbuck	(Intercept)	1.87	0.25	0.0E+00	1.38	2.35	NA
	Availability	0.44	0.17	1.2E-02	0.10	0.78	1.00
	Farming vs residential	0.30	0.21	1.6E-01	-0.12	0.72	0.51
	Diversity	0.44	0.12	1.8E-04	0.21	0.67	1.00
	Hydromorphy	-0.49	0.19	9.7E-03	-0.87	-0.12	0.95
	Urbanisation	-0.22	0.15	1.5E-01	-0.51	0.08	0.51
	Connectivity	0.37	0.21	8.1E-02	-0.05	0.78	0.65
	Dogs	0.05	0.18	8.0E-01	-0.31	0.41	0.26
	Humans	0.20	0.18	2.8E-01	-0.16	0.56	0.40
Common duiker	(Intercept)	-1.54	0.20	0.0E+00	-1.93	-1.15	NA
	Availability	0.16	0.09	6.7E-02	-0.01	0.34	0.68
	Farming vs residential	0.31	0.13	1.6E-02	0.06	0.57	0.92
	Diversity	0.19	0.11	8.2E-02	-0.02	0.39	0.63
	Hydromorphy	-0.16	0.18	3.7E-01	-0.52	0.19	0.35
	Urbanisation	-0.44	0.21	3.3E-02	-0.85	-0.04	0.86
	Connectivity	-0.51	0.23	2.5E-02	-0.95	-0.06	0.87
	Dogs	0.17	0.15	2.5E-01	-0.12	0.46	0.42
	Humans	-0.07	0.16	6.4E-01	-0.39	0.24	0.27
Grysbok	(Intercept)	-1.82	0.22	0.0E+00	-2.26	-1.38	NA
	Availability	0.07	0.09	4.3E-01	-0.10	0.24	0.33
	Farming vs residential	0.33	0.13	1.4E-02	0.07	0.59	0.92
	Diversity	0.20	0.11	6.9E-02	-0.02	0.42	0.67
	Hydromorphy	-0.14	0.19	4.5E-01	-0.50	0.23	0.32
	Urbanisation	-0.54	0.23	2.0E-02	-1.00	-0.08	0.92
	Connectivity	-0.73	0.24	3.0E-03	-1.20	-0.25	1.00
	Dogs	0.01	0.15	9.3E-01	-0.28	0.30	0.25
	Humans	0.02	0.15	8.8E-01	-0.28	0.33	0.25
Porcupine	(Intercept)	1.17	0.17	0.0E+00	0.83	1.51	NA
	Availability	0.28	0.11	1.1E-02	0.06	0.50	0.95

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Farming vs residential	-0.18	0.14	1.9E-01	-0.46	0.09	0.45
Diversity	0.30	0.10	2.5E-03	0.11	0.49	1.00
Hydromorphy	-0.50	0.17	3.6E-03	-0.84	-0.16	0.99
Urbanisation	-0.24	0.13	7.9E-02	-0.50	0.03	0.64
Connectivity	0.22	0.18	2.2E-01	-0.13	0.57	0.43
Dogs	0.21	0.17	2.1E-01	-0.12	0.54	0.45
Humans	0.15	0.16	3.5E-01	-0.16	0.45	0.35

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## Chapter 3

### Combining camera traps and citizen approach to better understand the persistence of African mammals in multifunctional landscapes



We collected data thanks to a CTs grid and an online survey but we did not assess yet how comparable they were, which is the objective of the manuscript 4. By averaging the responses per the 5 km<sup>2</sup> cell of the CTs grid, we showed that it was possible to compare the detection obtained with the two methods. The concordance was greater for the detection of the larger species than for smaller ones, in particular, the mongooses were difficult to identify by the survey participants. Bearing in mind the constraints and biases of each method, we combined the two data sets in the manuscript 5 to evaluate the traits which allowed mammal species to persist in the anthropogenic landscapes of the GRBR. Our results showed that areas highly modified by humans were more favorable for generalist species than for strict carnivores and were mostly used by smaller species. Protected areas and natural habitats did not select for any specific traits, confirming their role as refuge for all mammal species. Manuscript 5 is a draft form which still requires further investigation. The next two manuscripts have not been peer-reviewed and the English must be corrected before submission.

Manuscript associated to the chapter 3:

- Manuscript 4: **Alice Bernard**, Chloé Guerbois, Jan A. Venter and Hervé Fritz. Comparing local ecological knowledge with camera trap data to study mammal occurrence in anthropogenic landscapes of the Garden Route Biosphere Reserve
- Manuscript 5: **Alice Bernard**, Chloé Guerbois, Jan A. Venter and Hervé Fritz. Combining local ecological knowledge with camera traps to assess the link between African mammal life history traits and their use of anthropogenic landscapes

## Manuscript 4

# Comparing local ecological knowledge with camera trap data to study mammal occurrence in anthropogenic landscapes of the Garden Route Biosphere Reserve

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## Abstract

Accurate information on wildlife occurrence in anthropogenic landscapes is essential to develop adequate conservation measures, and monitoring methods must be adapted to their contexts and objectives. However, monitoring multiple mammal species in multifunctional landscapes can be challenging because of the diversity of land-uses and species behavioural responses. We compared data obtained from camera traps with data gathered through an online survey to document the presence of mammal species in mosaic landscapes on the Garden Route, South Africa. They were respectively able to detect 15 and 16 species, with one more species in the survey, the common duiker (*Sylvicapra grimmia*). Both methods effectively detected most large species, whereas results were less consistent for smaller species and mesocarnivores in particular. Combining methods enabled to get more robust estimates of absence and confirmed presence indicated by informants. Informants with above average ecological knowledge were good sentinels for monitoring mammal species, while extending the spatial coverage of the study. The choice of the best method depends on the species, monitoring objectives, and available resources. Bearing in mind the limitations of each method, camera traps and online survey complement each other to give a better picture of the mammal community in anthropogenic landscapes, expanding both spatial coverage and species sighting sample sizes.

**Key words:** Wildlife monitoring, participatory research, habitat transformation, combined methods, mammal ecology, biosphere reserve, wildlife conservation

## 1 | Introduction

Humans have shaped natural ecosystems and habitats as a result of land-use and transformation (Ellis et al., 2021). A fundamental question for conservation science and practices is understanding the impact of these transformations on biodiversity (Corlett, 2015). Mammals, among others, are facing numerous human-induced threat such as habitat alteration, hunting, climate change or the introduction of invasive species (Atwood et al., 2020). Their movements have been considerably reduced by human modification of natural habitats and increasing human footprint (Tucker et al., 2018). Presently, 15.95% of the terrestrial land is protected (UNEP-WCMC et al., 2020) but the lack of connectivity between them often forces animals to use anthropogenic matrices at large scale (Brennan et al., 2022). The concept of 'shared Earth' developed by Obura et al. (2021) proposes to actively share the present 55% of the terrestrial land dominated by humans but not entirely transformed, by redesigning landscapes to make them suitable for wildlife. The rest of the surface being divided between untouched preserved areas (25%), *i.e.* mostly protected areas and areas exclusively developed for humans (21%) such as cities (Obura et al., 2021). In this context of rethinking transformation of the terrestrial areas by humans and their activities, it is necessary to understand which species could effectively use the diversity of anthropogenic matrix. There are several potential survey methods that can be used to monitor the presence of mammals, and they all have their own biases (Brittain et al., 2022; Hofmeester et al., 2019).

Camera trap (CT) surveys are a commonly used non-invasive method for monitoring wildlife over a long period of time (O'Connell et al., 2011). CTs data provide reliable information on the frequency of occurrence, time of the day and of year of the species (O'Connell et al., 2011). However, this method can become costly in terms of material investment, as well as for fieldwork and staff required for servicing, and processing the data collected (Brittain et al., 2022). Detections often depend on species ecological characteristics such as home-range size and density (Hofmeester et al., 2019), but are not seasonally biased as CTs record continuously (Zwerts et al., 2021). The set-up can highly influence the detection, which for instance can vary between vegetation types; e.g. detection rate is often lower in closed than open habitats (Sollmann et al., 2013).

Anthropogenic landscapes are characterized by the presence of people who could intentionally or unintentionally observe and monitor wildlife around them. Large-scale citizen sciences projects are flourishing all over the world (Dickinson et al., 2012). Several methods can be used to mobilize local knowledge such as interviews, questionnaires, participatory mapping or diaries (Jones et al., 2008; Pédarros et al., 2020; White et al., 2005). They allow the collection of a large amount of data, at relatively low cost and often with a broad coverage to answer ecological questions (Dickinson et al., 2012). Local Ecological knowledge (LEK) can also provide information on people's practices, values or perceptions (Bennett et al., 2017). LEK has been shown to be a cost-effective tool for studying the presence of mammals (Burt et al., 2021; Turvey et al., 2013). Furthermore, involving people in the research protocols could help to promote reconnection with the natural world, while allowing the researchers, and society at large, to benefit from their local knowledge (Obura et al., 2021). The detection of a species is highly dependent on the observer and can vary with season and species behavior (Boakes et al., 2010; Msoffe et al., 2007; Pearse et al., 2015). Humans can detect mammal species using a range of direct (sightings) and indirect cues such as tracks, scats or hairs which can remain

for longer in the landscape (Zwerts et al., 2021). However, incorrect identifications are difficult to detect (McKelvey et al., 2008) and the reliability of LEK has been questioned (Caruso et al., 2017), even though in many instances well designed and analyzed, surveys provide trustworthy information (Jones et al., 2008; Petracca & Frair, 2017).

Few studies have simultaneously compared the detection outcomes of CTs and LEK in human-dominated mosaic landscapes (Brittain et al., 2022; Caruso et al., 2017; Schaller et al., 2012; Zwerts et al., 2021). The choice of the best method depends on the targeted species, the population metrics that needs to be evaluated, the species identification and the resources available for the project (Zwerts et al., 2021). Therefore, it appears necessary to run site-specific studies to understand which method will be the most effective (Brittain et al., 2022; Swan et al., 2014), or how combine them best. Different methods would not produce the same level of information and combining methods could provide complementary data to document a situation, and improve the understanding of a phenomenon (Brittain et al., 2022; Schaller et al., 2012; Service et al., 2014).

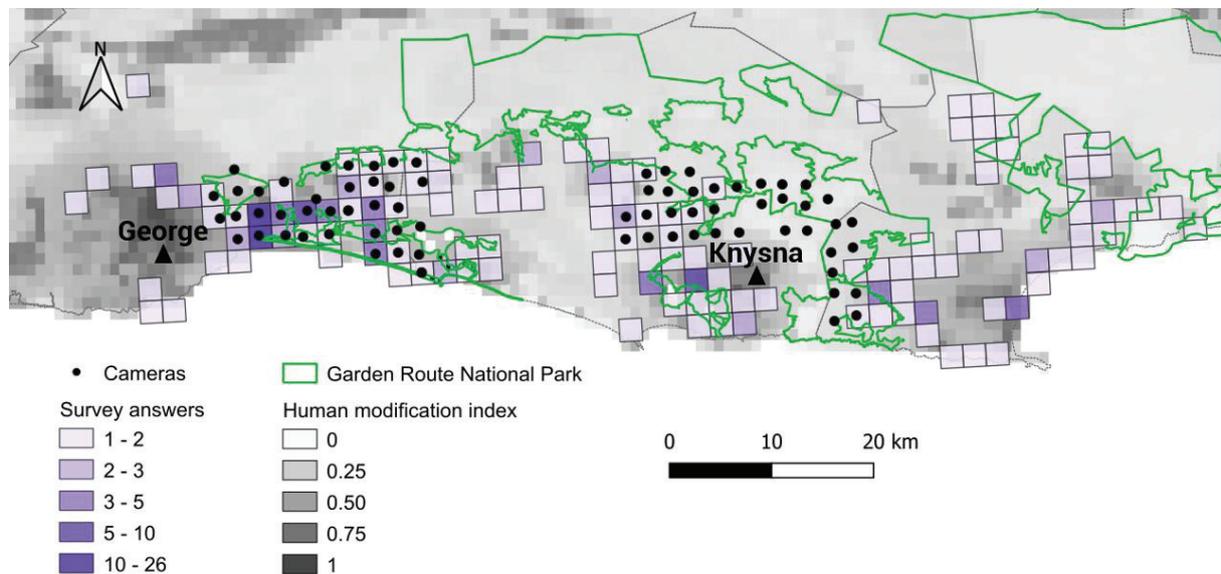
Here we used two independent data sets to compare CTs and LEK consistency in detecting wild mammal species occurrence in the mosaic landscapes of the Garden Route Biosphere Reserve (GRBR), in South Africa, and tested hypotheses which could explain the discrepancies. Mammals are good study models as they are visible and, therefore, generally easily identifiable, and represent a variety of size, diet and ecological requirements (Santini et al., 2019). The mammal community of the GRBR is a fair representation of this diversity and is composed of rare to common species (Baard et al., 2015). We examined a set of variables that we suspected of biasing detection to explain the discrepancies between the two methods: the level of human modification of the landscape (Human Modification Index), knowledge of respondents and some species traits (diet group, body mass, diurnality). We expected both methods to be comparable, and to be consistent for large mammal detections, while CTs would be more reliable in detecting small body mass and nocturnal species. We predicted that LEK would be more efficient in highly modified landscapes, *i.e.* with more people, and will provide more data for rare species, especially if respondents have a good ecological knowledge. On the other hand, CTs were predicted to be more efficient in detecting species in less disturbed areas as human observers would be by definition less present.

## 2 | Materials and methods

### 2.1 | Study area

The study took place in the GRBR in the Western Cape, on the south-eastern coast of South Africa. Nested between the Indian Ocean and the Outeniqua mountains (Figure 1). The region is highly attractive to national and foreign dwellers (Guerbois et al., 2019). The number of residences has increased significantly in recent years and the population is expected to continue to grow in the coming years (Guerbois et al., 2019; Western Cape Government, 2019). Human-modified landscapes are associated with multiple land-uses such as exotic tree plantations, crop and dairy farming, urban and peri-urban developments, and a vast road network (Baard et al., 2015; SANParks, 2020). The Garden Route National Park (GRNP), an unfenced protected area managed by South African National Parks was established in 2009. The park is mostly open access for visitors, who can enjoy outdoor activities such as

canyoning, mountain biking or hiking, but natural resource harvesting is prohibited or strictly regulated (Roux et al. 2020).



**FIGURE 1** Study site in Garden Route Biosphere Reserve, South Africa. The number of responses to the survey (purple gradient) and locations of the camera traps (black dots) have been superimposed on the same 5 km<sup>2</sup> grid. We used the human modification index pixel map in the background and plotted the boundaries of the Garden Route National Park in green.

## 2.2 | Data collection

### 2.2.1 | Camera traps (CTs)

We took advantage of a field set-up composed of a grid of 75 CTs (Figure 1), where 30 CTs were set-up in the GRNP the rest (45 cameras) were set-up in human-dominated areas (**manuscript 2**). We used two models of CTs: 33 Bushnell Trophy Cam HD Aggressor and 41 SPYPOINT Force Dark. The CT protocol followed a standardized method adopted in the Snapshot Safari Project (Pardo et al., 2021). CTs were positioned to detect medium to large mammals as close as possible to the center of a regular 5 km<sup>2</sup> (2.23\*2.23 km) grid. CTs were set-up on a game trail, at a height of 50 cm above the ground and mainly on trees (**manuscript 1**). Each CT was programmed to take a series of three images within 1 to 5 seconds of each other. CTs were serviced every two to three months to change the batteries and SD cards. The CTs monitoring ran from the 2nd of February 2021 to the 20th of May 2022, during which four CTs were stolen.

### 2.2.2 | Online survey

We conceived an online survey questionnaire to assess the presence of wild mammals and describe characteristics of private properties of the GRBR (**manuscript 3**). This survey was designed to gain more knowledge on species occurrence in human-dominated landscapes (Appendix 1), and targeted landowners of the GRBR. After having been piloted several times and translated, the survey was sent using mailing lists obtained by conservation agencies such as CapeNature, SANParks, Wildlife and Environment Society of South Africa, as well as local conservancies, WhatsApp and Facebook groups. We also advertised the online survey in local

newspapers (George Herald's, The Edge). The survey was accessible online from November 2021 to March 2022, in both English and Afrikaans. We sent several follow-ups to increase our sample size. This research was approved by Nelson Mandela University ethic committee (H20-SCI-SRU-002). Both methods were conducted in the same year to avoid variations because of temporal changes.

Species presence was assessed by a question on the frequency to which the respondent saw the species on their property. They had multiple choices for the species and the frequency of sightings: not at all, not anymore, rarely (once a year), occasionally (once a month), frequently (once a week), very frequently (every day). Respondents could also select general categories when they did not know the differences between species (e.g. mongoose, genets even though the family includes different species). For each question, respondents were given a choice of three species. Participants had to position their residence on the exact same grid of 5 km<sup>2</sup> cells used for the CTs; no exact geographical or global positioning (GPS) location had to be shared thus preserving the anonymity of the participants (Figure 1). They also indicated their main activities, involvement in conservation initiatives and other information about them and their properties. The ecological knowledge of the respondents was tested by asking four questions in the survey. Two were based on identifying a species using a photograph: an herbivore (blue duiker, *Philantomba monticola*) and a mesocarnivore (Cape grey mongoose, *Herpestes pulverulentus*). The third required respondents to identify the track of a carnivore (caracal, *Caracal caracal*), and the fourth to identify the scat of a herbivore (porcupine, *Hystrix africaeaustralis*). A more detailed description can be found in the **manuscript 3**.

## 2.3 | Data processing and analysis

We received 247 complete answers and gathered 12,002 independent photos of wild mammal species. Thirty-five cells were common to the two data sets, *i.e.* with a CTs and at least one answer from the survey. Only these 35 cells were considered for the following analyses, corresponding to 35 CTs and 95 answers.

### 2.3.1 | Estimating wildlife occurrence

#### 2.3.1.1 | From camera traps

The photographs were manually tagged with all species identified (mammals, birds, reptiles, humans, their activities and domestic animals), firstly by using digiKam (digikam team, 2001), then with the online software TrapTagger (Osner, 2022). For this analysis, we focused on mammal species >500g. Empty photographs and pictures with birds, rodents, humans, their activities and domestic animals were not considered. When similar species were detected we filtered the data to keep only one photograph every 30 minutes and ensure independent events. We grouped the three species of mongooses photographed in the area (Cape grey mongoose, large grey mongoose *Herpestes ichneumon* and water mongoose *Atilax paludinosus*) under the category 'mongoose', to match the fact that respondents had difficulties in identifying animals at the species level in the survey. To compare the frequency of occurrence from CTs and the survey, we built a CT detection matrix to indicate each species' monthly and weekly presence in each cell. When there was no detection by CTs we classified the frequency of occurrence as 'never'. When the species was detected in more than three different months, we classified the frequency of occurrence as 'occasional' and in less than

three months as 'rare'. Species detected in more than half of the weeks surveyed were considered as 'frequent'. We did not classify species as very frequent as no species was photographed daily.

#### 2.3.1.2 | *From online survey*

We transformed the frequency of occurrence for each species to obtain a presence/absence variable. When a respondent did not declare a species or reported that a species no longer occurred on their property, we assigned the variable a value of 0 (absence). When a species occurred very frequently (every day) or frequently (once a week), we assigned the value of 3 (the two categories were grouped to match CTs data, for which species were never seen every day), occasionally was assigned a value of 2 (once a month) and rarely (once a year) of 1. As a given cell could be related to several respondents, we averaged the frequency of occurrence for each species on each cell, and considered the species was present if the score was equal or above to 1 and assigned a value of 1 for all presence. We assigned a value of 0 to indicate an absence when the score was under 1. Because mongooses and genets were difficult to identify at species level we used the general categories 'mongooses' (including the Cape grey mongoose, large grey mongoose and water mongoose) and 'genets' (including the large-spotted genet and small-spotted genet) in subsequent analyses. Only the large-spotted genet has been recently recorded in the area and detected with the CTs, although both species are listed as potentially occurring (Baard et al., 2015).

#### 2.3.2 | Candidate variables to assess detection bias

We tested a set of variables which we hypothesized could explain discrepancies of detection between the two methods describing characteristics of the species, the cells or the respondents. We first selected species traits that we anticipated to affect the probability of detection of mammal species in anthropogenic environments (Figure S1). As diet flexibility could influence the ability of a species to adapt to a new environment (Hulme-Beaman et al., 2016), we used the EltonTraits database (Wilman et al., 2014) to extract data on the diet of each studied species and classified them as carnivores, herbivores, omnivores and mesocarnivores. We completed our information using PanTHERIA database (Jones et al., 2009) to extract adult body mass and information on the diurnality (diurnal or nocturnal). To account for spatial heterogeneity at the scale of the cell and assess level of human modification of the landscape covered by the survey, we calculated the mean Human Modification Index (HMI, 1-km resolution), in each 2.23 \* 2.23 km cell ('aggregate' function, 'stats' package). The values range from 0 to 1 (Kennedy et al., 2020). A value close to 0 indicated no human modification and a value close to 1 indicated high modifications of the terrestrial land (Kennedy et al., 2020). Finally, to assess heterogeneity between the respondents, at the property scale, we attributed them an ecological knowledge score by averaging the calculated score at the knowledge questions for each respondent of the cell. We obtained a variable between 0%, when they responded wrong to each question and 100%, when they responded correctly to all questions.

#### 2.3.3 | Data analyses

We compared the response of each respondent with the information given by the CT of the same cell. When the species was detected with the two methods, we coded the pair CT and.

survey as a 'presence' (P); when both methods did not detect the species, we coded it as an 'absence' (A); when a species was detected only with the CTs, we coded it as a 'presence CT' (PC) and when a species was detected only with the survey, we coded it as a 'presence survey' (surveys; Figure S3). As we were interested in the discrepancy between the methods, we grouped P and A as they represented 'similar detection' (S). We compared the three categories S, PC and PS by running a multinomial analysis ('multinom' function, 'nnet' package; Venables & Ripley, 2002). We tested the five previously described variables that could explain the discrepancies between the two methods: HMI value in the cell, average ecological knowledge score of respondents in the cell, body mass, diet and diurnality of each species. All the analyses were performed on R (R Core Team, 2020). We used the package 'ggplot2' for graphical representations (Wickham, 2016).

### 3 | Results

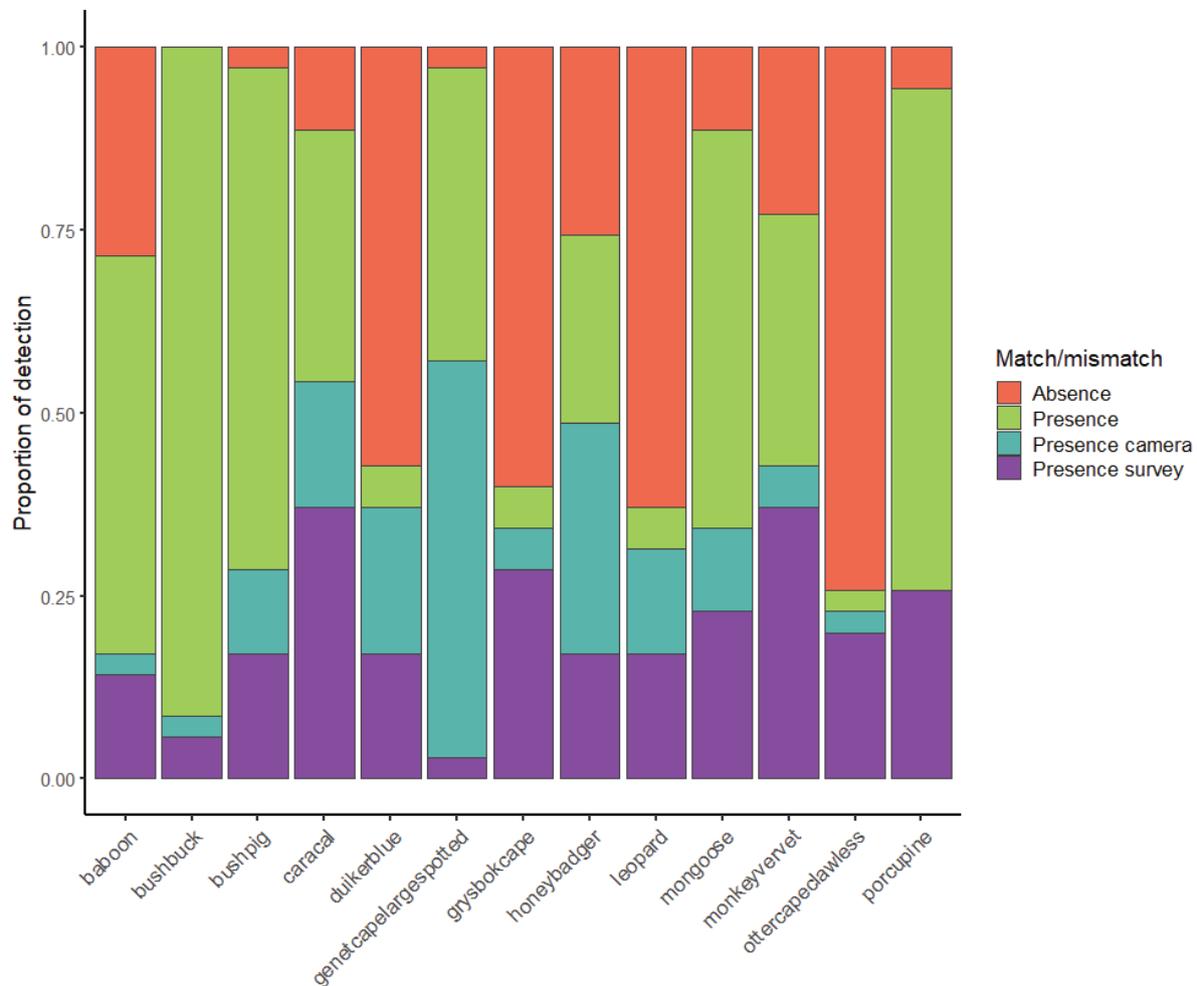
#### 3.1 | Monitoring efforts

Sixteen species were detected by both methods (Tables 1 and S1). Six species were strictly nocturnal and their body mass ranged from 0.8 to 52 kg (Table 1). Only the common duiker was not detected by CTs, and was excluded from the analysis (Tables 1 and S1). The survey detected all species, including species rarely detected by CTs (otter, grysbok) on more sites (Table S1). On the contrary, the genet and the blue duiker were detected on more sites with CTs (Table S1). The two methods were consistent in the number of sites for the bushbuck and the bushpig (Table S1). The number of responses per cell ranged from 1 to 24 (Figure 1 and S2). The gradient of knowledge score range from 0 to 100%, with an average score of 58% (Figure S1). The cells covered a gradient of land-use human modification, *i.e.* HMI value ranged from 0.07 to 0.69.

**TABLE 1** Summary table of the detection of 16 species on the 35 common cells.

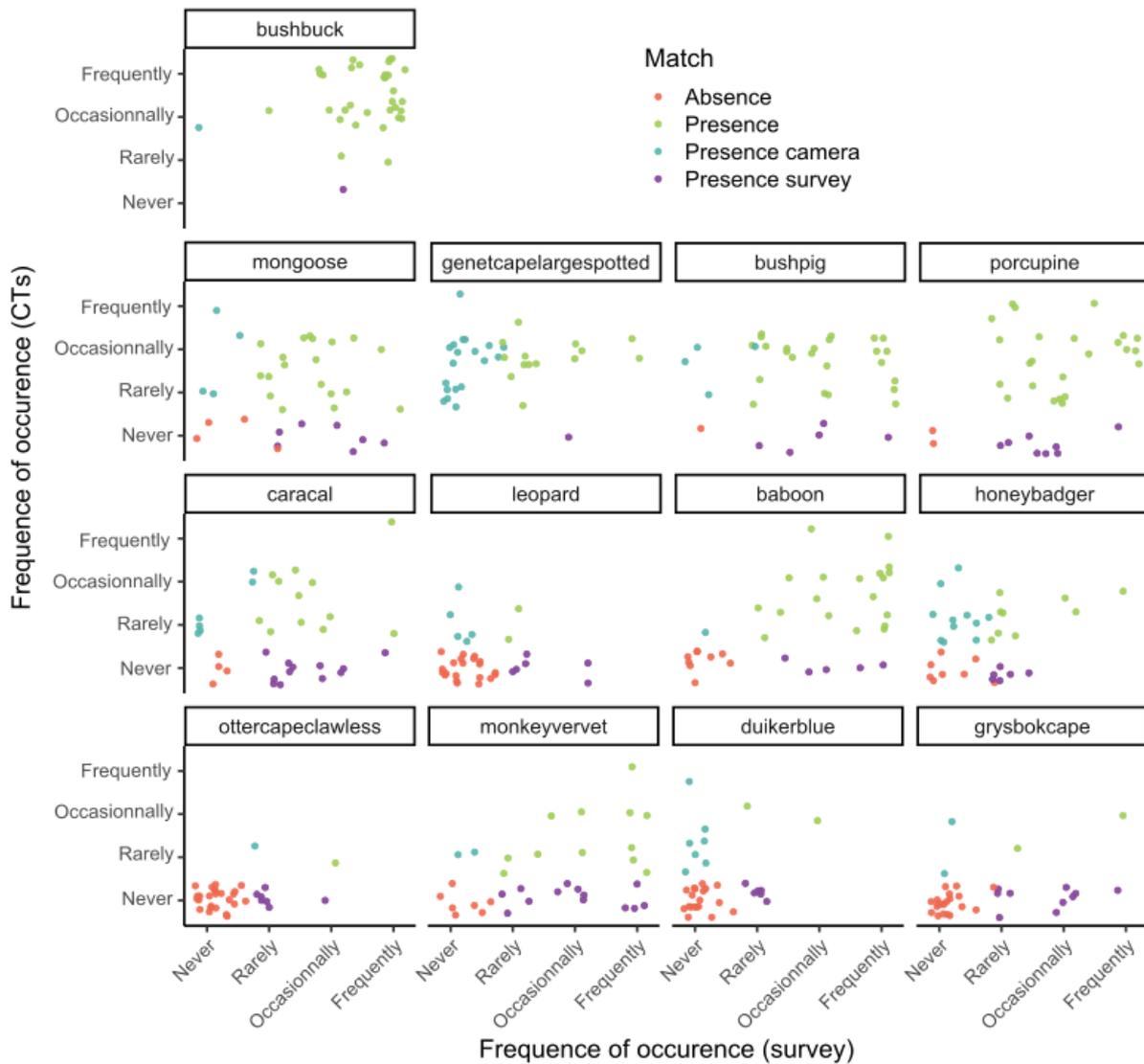
English name	Scientific name	Diet	Body mass (kg)	Diurnal/Nocturnal
<b>South African large-spotted genet</b>	<i>Genetta tigrina</i>	carnivore	2	Nocturnal
<b>Caracal</b>	<i>Caracal caracal</i>	carnivore	13.7	Diurnal
<b>Leopard</b>	<i>Panthera pardus</i>	carnivore	52	Diurnal
<b>Cape grysbok</b>	<i>Raphicerus melanotis</i>	herbivore	10.2	Nocturnal
<b>Blue duiker</b>	<i>Philantomba monticola</i>	herbivore	4.9	Diurnal
<b>Common duiker</b>	<i>Sylvicapra grimmia</i>	herbivore	15.6	Nocturnal
<b>Cape porcupine</b>	<i>Hystrix africaeaustralis</i>	herbivore	14.9	Nocturnal
<b>Bushbuck</b>	<i>Tragelaphus scriptus</i>	herbivore	43,2	Diurnal
<b>Mongoose: Cape grey mongoose, Large grey mongoose, Water mongoose</b>	<i>Herpestes pulverulentus</i> , <i>Herpestes ichneumon</i> , <i>Atilax paludinosus</i>	mesocarnivore	0.8	Diurnal
<b>Honey badger</b>	<i>Mellivora capensis</i>	mesocarnivore	8.5	Diurnal
<b>African clawless otter</b>	<i>Aonyx capensis</i>	mesocarnivore	19	Nocturnal
<b>Vervet monkey</b>	<i>Cercopithecus pygerythrus</i>	omnivore	5	Diurnal
<b>Chacma baboon</b>	<i>Papio ursinus ursinus</i>	omnivore	17.7	Diurnal
<b>Bushpig</b>	<i>Potamochoerus larvatus</i>	omnivore	48.8	Nocturnal

The match between the two methods depended on the species (Figure 1). Both methods similarly detected common species such as the bushbuck, baboon and porcupine as well as rare species, e.g. the grysbok, leopard or otter (Figure 1). The two methods were mostly inconsistent for detecting the caracal, honey badger, vervet monkey and especially the genet (Figure 1).



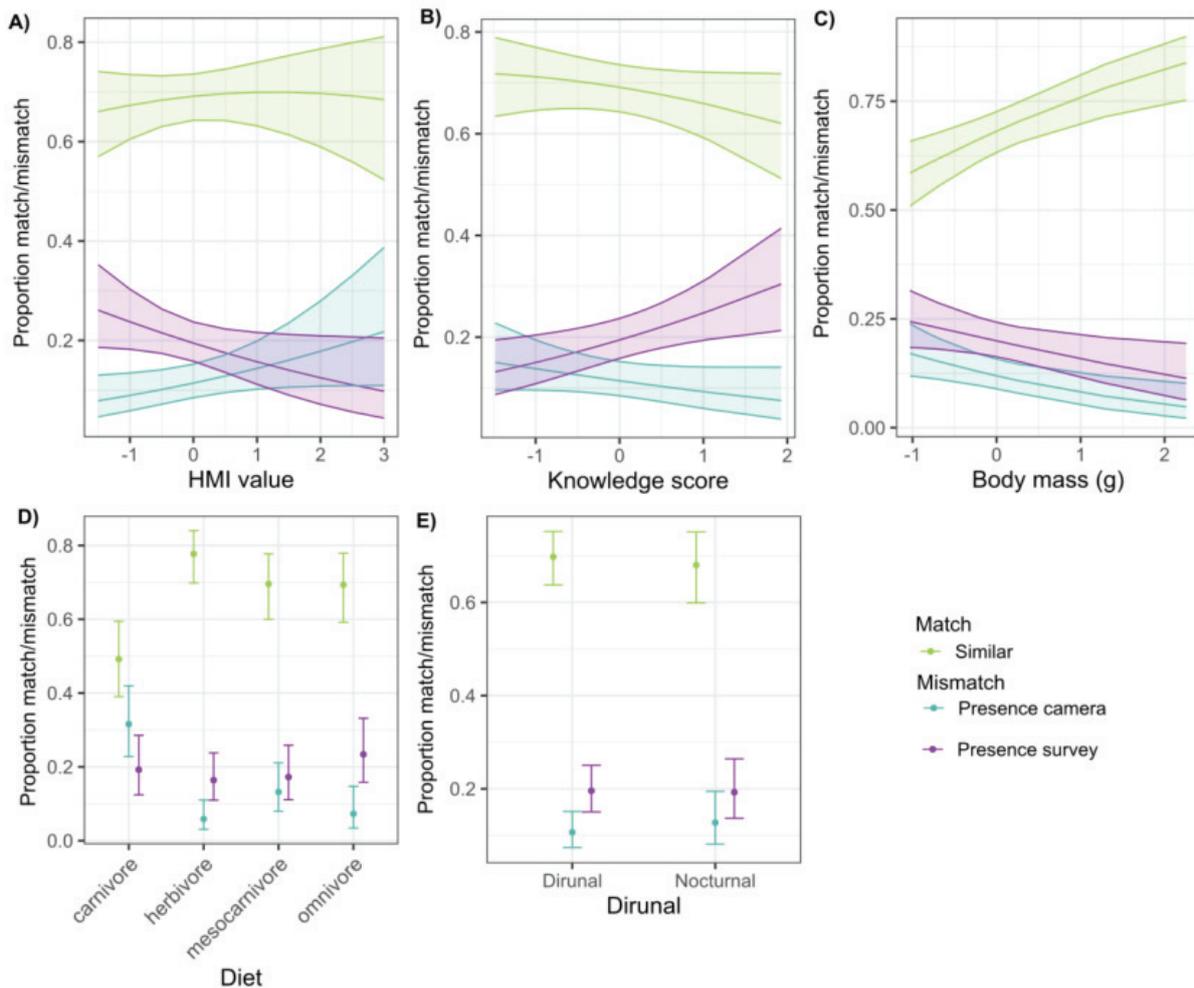
**FIGURE 1** Representation of the proportion of detection per species that were the same in a given cell according to both methods: present (P, in green) or absent (A, in red) or different: presence camera only (PC, in blue) or presence survey only (PS, in purple).

The absence of detection reported by informants at the scale of the cell and the non-detection by CTs seemed to be in accordance (Figure 2). The methods appeared consistent for common species such as the bushbuck and the baboon, as well as rare species such as the leopard (Figure 2). The survey often provided presence data for carnivores whereas CTs did not (Figure 2). CTs were more efficient than respondents for detecting the genet, blue duiker and honey badger. Reciprocally, cases where species were detected by respondents but not the CTs included the caracal, vervet monkey, blue duiker or grysbok (Figure 2).



**FIGURE 2** Representation of the frequency of detection by the CTs and the survey categories, grouped by species in a given cell. The colors represent if the detection were the same between the methods.

The probability of both methods detecting the presence of a species at a site was greater than the one with no matching detection, suggesting that the methods were mostly consistent (Figures 2, 3, and S3, Table S2). The two methods were both less efficient at detecting small species than larger ones (Figures 3 and S3, Table S2). Most of the presence detected exclusively by the survey occurred on the cell of owners which better knowledge (Figures 3 and S3, Table S2). The most inconstancy occurred for detecting carnivores (Figures 3 and S3, Table S2). CTs were less effective for detecting omnivores and herbivores than respondents of the survey (Figures 3 and S3, Table S2). The level of anthropogenic modification of the cell (HMI value) did not affect the probability of a match between the two methods, nor did the diurnality of the species (Figures 3 and S3, Table S2).



**FIGURE 3** Representation of the predicted values from the multinomial modelling, for the five explanatory variables: A) HMI value, B) knowledge score, C) body mass, D) diet, and E) diurnality. The colours represent the match and mismatches between methods: similar detections in green, detection on CTs only in blue and in the survey only in purple.

## 4 | Discussion

Reliable information on mammal use of anthropogenic landscape is necessary to develop appropriate conservation measures. CTs and LEK methods enabled the detection respectively of 15 and 16 mammals of the Garden Route Biosphere Reserve which persist in this mosaic of landscapes. Compared with CTs, LEK gave a good indication of the species occurrence. Both methods had a better match for the detections of larger species. Respondents with better ecological knowledge detected more species than others, and more than CTs. Respondents with more ecological knowledge were good 'sensors' to monitor mammal species, as shown in other contexts (Burt et al., 2021). However, the survey did not seem appropriate for small carnivores such as mongoose and genets. When people detected a species that had not been detected by a CT, either the CT had missed the species if it had not passed in front of it, or the CT may have been placed in a location that the species did not use (Hofmeester et al., 2019).

Informants may also have detected the species with indirect signs such as tracks or scats (Zwerts et al., 2021). In the supplementary material of **manuscript 3** (Table S2), we showed that the percentage of sightings and indirect cues of detection varied between species, with most respondents detected bushbuck by sightings (92%) but blue duiker (39% of sightings) or leopard (33% of sightings) were mostly detected by indirect signs. Otherwise, informants may have misidentified the species and confounded with another species, which is unverifiable (McKelvey et al., 2008). Inconsistency between the two methods suggested that species such as carnivores (caracal and leopard), the otter, the blue duiker, the common duiker or the grysbok would require specific monitoring programs. However, combining methods could enable scientists to get more robust estimates of absence and confirmed the presence of species indicated by informants (**manuscript 5**).

It is impossible to conclude that one method is generally better than the other. Our result suggested that the reliability of the two methods depend on the species (Anadón et al., 2010; Caruso et al., 2017). As suggested by other studies, participatory approaches gave more information for rare species, where CTs probability of detection was low (Brittain et al., 2022; Burt et al., 2021). Wildlife monitoring requires time investment and a protocol adapted to their behavior and ecology (Hofmeester et al., 2019; Sollmann et al., 2013). CTs do not necessarily have the best results for rare and cryptic species but are important to monitor places where humans do not go as shown with the example of the blue duiker. Combining monitoring methods seem critical for these species (Brittain et al., 2022; McKelvey et al., 2008; Zwerts et al., 2021). Survey data are often more subjective and depend on the capacity of the respondent to identify correctly and remember a species (Zwerts et al., 2021). Humans can have a detection bias towards certain species, such as charismatic or conflictual, because of their ecology and experience (Boakes et al., 2010; Martínez-Martí et al., 2016; Msoffe et al., 2007). This bias should be minimal in our case as we only kept species detected by at least 15% of the respondents. On the contrary, with CTs, if the species passes by, the identification can be verified (Hofmeester et al., 2019). CTs survey have biases in detection, which can be reduced in the field and corrected in the analyses commonly used, such as in occupancy models (Hofmeester et al., 2019; MacKenzie & Bailey, 2004). However, species behave differently, so using CTs following a standardized protocol may not be the more appropriate for all of them (Hofmeester et al., 2019). Discrepancies between the two methods could be explained by the large scale of 5km<sup>2</sup>, a scale often use in CTs survey to ensure spatial independence between sites (Pardo et al., 2021), but possibly inappropriate for species depending on specific localized micro-habitats or with relatively small home-ranges or territories. Humans move across the landscape whereas CTs are fixed, which could also explain some differences in detection (Zwerts et al., 2021). Humans might be biased towards the areas they use most but their likelihood of encountering a species increases with their mobility in the landscape. Most importantly, many people are using these anthropogenic landscapes, so there is a high potential for species detection, especially on private properties where people are spending more time, increasing the chances of detection (Pédarros et al., 2020). On the contrary, CTs have a small surface of detection (Zwerts et al., 2021). People can cover a much larger area than CTs, at a lower cost (Zwerts et al., 2021). As previous authors, we recommend combining several methods to better understand the animal distribution and activities over large mosaic landscapes (Anadón et al., 2010; Burt et al., 2021). Furthermore, our study highlighted the disparity of knowledge among the respondents and the necessity of assessing people's

knowledge to define data reliability. To obtain reliable data, observers must have a good knowledge of the species they can detect (Camino et al., 2020). In wide-ranging surveys, without any selection criteria for respondents, it may be useful to apply a threshold of acceptability of the data based on people's knowledge and frequency of citation of the species (Burt et al. 2021). Providing natural history and ecological education would be very useful to increase the proportion of trustable informants in a given area.

The two methods' design conception, needs and costs (material, staff, fieldwork) were different. The survey required more time in the conception phase, whereas CTs required a lot of time for the data collection and processing (Zwerts et al., 2021). We piloted the questionnaire with 20 landowners to develop a final version, well adapted to the context of GRBR and relevant to most participants. LEK protocols, especially online ones, must be piloted to ensure that the data can be trusted. The survey data were collected in 4 months, whereas the CTs survey ran for one year. Both methods required time for data cleaning and processing. For a research project with little financial support or staff, the survey is a great tool for a quick assessment of the presence of mammals in the landscape (Brittain et al., 2022), and can add information about resources used by animals on properties, hence contributing to a better understanding of coexistence processes (**manuscript 3**). Furthermore, the two methods did not provide the same level of information on ecological and anthropogenic variables (**manuscripts 2 and 3**). For example, the survey could offer more precise information on human practices than what can be gathered by looking at the proximity of the CTs (**manuscripts 2 and 3**). CTs could offer a better understanding of human activities and their immediate disturbances, as well as the presence of cats or dogs (domestic or feral) as they photograph them passing through the CT. This could provide valuable information on their impact on wildlife (Parsons et al., 2016; Seymour et al., 2020). The two methods enabled to cover a larger and more diverse areas (**manuscript 5**). We mostly got answers from peri-urban areas with the survey, whereas CTs were mostly set-up in tributaries and farms. Using human observers to assess mammal presence is an asset to extend spatial coverage (Zwerts et al., 2021). All the farmers contacted for the CTs survey responded positively to be part of it, but it was less efficient to have them respond to the survey and only 10% of the respondents were doing commercial farming (**manuscripts 2 and 3**). CTs appeared to be a protocol adapted for people willing to be involved in conservation but without investing time effort in it. It was also a way to implicate them in research protocol and get their attention on conservation issues, which could be valuable to start working on sharing space with wildlife (Obura et al., 2021). Surveys are also a tool to involve people in conservation issues and are a good method for empowering local populations (Camino et al., 2020; Devictor et al., 2010). We experienced that survey respondents were mostly already involved in conservation initiatives (**manuscript 3**). By unravelling the level of human-wildlife coexistence in a given landscape, it would contribute to further promoting the concept of shared Earth (Obura et al., 2021).

We recommend combining a grid of CTs and observers at a 5 km<sup>2</sup> scale as it minimizes the risk of missing species, while extending the spatial diversity and coverage of the study, both within and between grid cells. To do so, the design of the methods need to be thought out in advance to have compatible and comparable protocols (Petracca & Frair, 2017). The choices must be made according to the targeted species, objectives and resources available for the project (Camino et al., 2020; Zwerts et al., 2021). The two approaches combined allowed to

target key stakeholders and start engaging in discussions about conservation with them (Camino et al., 2020; Devictor et al., 2010). Using transdisciplinary approaches should improve research relevance for conservation (Zwerets et al., 2021). This is a necessary first step to co-construct and design conservation measures to build a shared land between people and wildlife (Obura et al., 2021).

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## References

- Anadón, J. D., Giménez, A., & Ballestar, R. (2010). Linking local ecological knowledge and habitat modelling to predict absolute species abundance on large scales. *Biodiversity and Conservation*, 19(5), 1443–1454. <https://doi.org/10.1007/s10531-009-9774-4>
- Atwood, T. B., Valentine, S. A., Hammill, E., McCauley, D. J., Madin, E. M. P., Beard, K. H., & Pearse, W. D. (2020). Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances*, 6(32), eabb8458. <https://doi.org/10.1126/sciadv.abb8458>
- Baard, J., Durrheim, G., Hanekom, N., Hayes, J. S., Kraaij, T., Kruger, N., Ngubeni, N., Randall, R. M., Russell, I. A., Seydack, A. H. W., Smith, K., Van der Vyer, L., & Vermeulen, W. J. (2015). Garden Route National Park—State of knowledge.
- Bennett, N. J., Roth, R., Klain, S. C., Chan, K., Christie, P., Clark, D. A., Cullman, G., Curran, D., Durbin, T. J., Epstein, G., Greenberg, A., Nelson, M. P., Sandlos, J., Stedman, R., Teel, T. L., Thomas, R., Veríssimo, D., & Wyborn, C. (2017). Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation*, 205, 93–108. <https://doi.org/10.1016/j.biocon.2016.10.006>
- Boakes, E. H., McGowan, P. J. K., Fuller, R. A., Chang-qing, D., Clark, N. E., O'Connor, K., & Mace, G. M. (2010). Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLOS Biology*, 8(6), e1000385. <https://doi.org/10.1371/journal.pbio.1000385>
- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N., & Kremen, C. (2022). Functional connectivity of the world's protected areas. *Science*, 376(6597), 1101–1104. <https://doi.org/10.1126/science.abl8974>
- Brittain, S., Rowcliffe, M. J., Kentatchime, F., Tudge, S. J., Kamogne-Tagne, C. T., & Milner-Gulland, E. J. (2022). Comparing interview methods with camera trap data to inform occupancy models of hunted mammals in forest habitats. *Conservation Science and Practice*. <https://doi.org/10.1111/csp2.12637>
- Burt, C., Fritz, H., Keith, M., Guerbois, C., & Venter, J. A. (2021). Assessing different methods for measuring mammal diversity in two southern African arid ecosystems. *Mammal Research*, 66(2), 313–326. <https://doi.org/10.1007/s13364-021-00562-x>
- Camino, M., Thompson, J., Andrade, L., Cortez, S., Matteucci, S. D., & Altrichter, M. (2020). Using local ecological knowledge to improve large terrestrial mammal surveys, build local

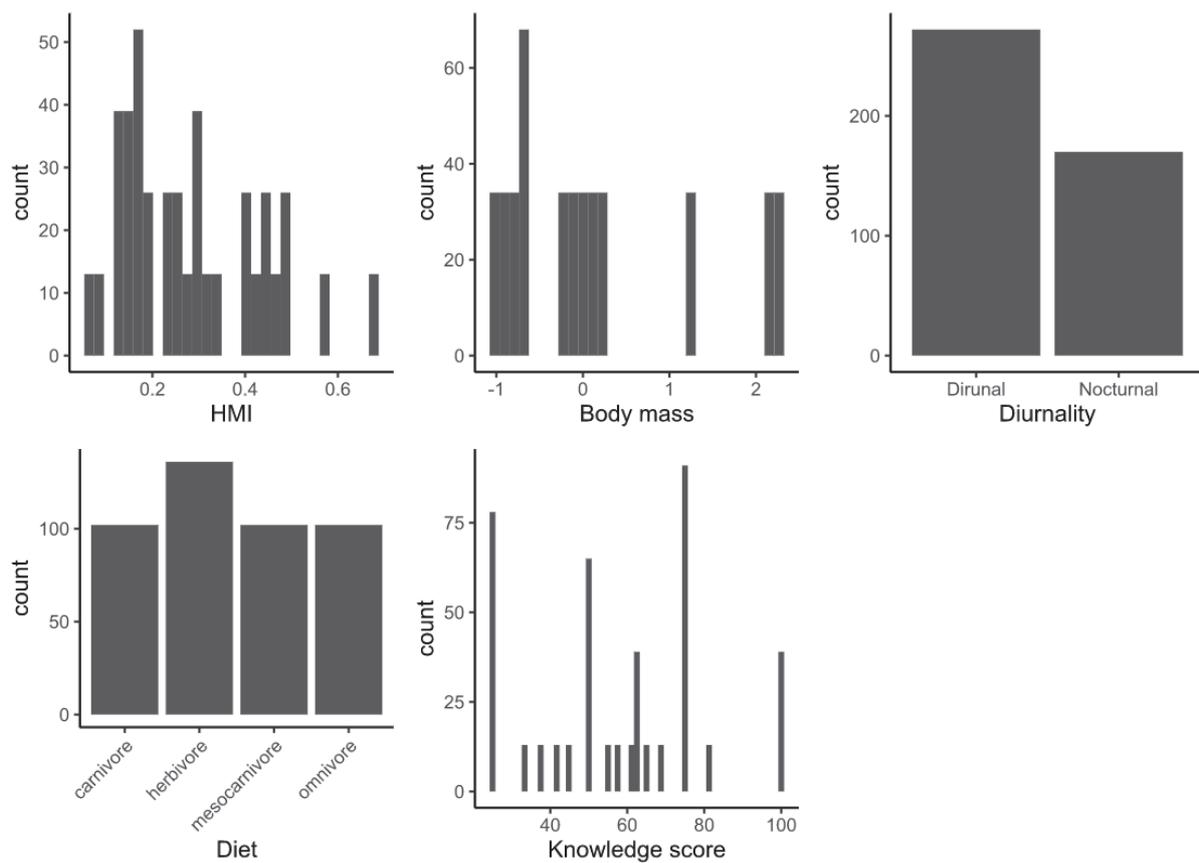
- capacity and increase conservation opportunities. *Biological Conservation*, 244, 108450. <https://doi.org/10.1016/j.biocon.2020.108450>
- Caruso, N., Luengos Vidal, E., Guerisoli, M., & Lucherini, M. (2017). Carnivore occurrence: Do interview-based surveys produce unreliable results? *Oryx*, 51(2), 240–245. <https://doi.org/10.1017/S0030605315001192>
- Corlett, R. T. (2015). The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, 30(1), 36–41. <https://doi.org/10.1016/j.tree.2014.10.007>
- Devictor, V., Whittaker, R. J., & Beltrame, C. (2010). Beyond scarcity: Citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions*, 16(3), 354–362. <https://doi.org/10.1111/j.1472-4642.2009.00615.x>
- Dickinson, J. L., Shirk, J., Bonter, D., Bonney, R., Crain, R. L., Martin, J., Phillips, T., & Purcell, K. (2012). The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10(6), 291–297. <https://doi.org/10.1890/110236>
- digikam team. (2001). DigiKam [Computer software]. <https://www.digikam.org/>
- Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, 118(17), e2023483118. <https://doi.org/10.1073/pnas.2023483118>
- Guerbois, C., Brady, U., de Swardt, A. G., & Fabricius, C. (2019). Nurturing ecosystem-based adaptations in South Africa's Garden Route: A common pool resource governance perspective. *Regional Environmental Change*, 19(7), 1849–1863. <https://doi.org/10.1007/s10113-019-01508-5>
- Hofmeester, T. R., Cromsigt, J. P. G. M., Odden, J., Andrén, H., Kindberg, J., & Linnell, J. D. C. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution*, 9(4), 2320–2336. <https://doi.org/10.1002/ece3.4878>
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, 31(8), 633–645. <https://doi.org/10.1016/j.tree.2016.05.001>
- Jones, J. P. G., Andriamarivololona, M. M., Hockley, N., Gibbons, J. M., & Milner-Gulland, E. J. (2008). Testing the use of interviews as a tool for monitoring trends in the harvesting of wild species. *Journal of Applied Ecology*, 45(4), 1205–1212. <https://doi.org/10.1111/j.1365-2664.2008.01487.x>
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90(9), 2648–2648. <https://doi.org/10.1890/08-1494.1>
- Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2020). *Global Human Modification of Terrestrial Systems*. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/edbc-3z60>
- MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9(3), 300–318. <https://doi.org/10.1198/108571104X3361>
- Martínez-Martí, C., Jiménez-Franco, M. V., Royle, J. A., Palazón, J. A., & Calvo, J. F. (2016). Integrating occurrence and detectability patterns based on interview data: A case study for

- threatened mammals in Equatorial Guinea. *Scientific Reports*, 6(1), 33838. <https://doi.org/10.1038/srep33838>
- McKelvey, K. S., Aubry, K. B., & Schwartz, M. K. (2008). Using Anecdotal Occurrence Data for Rare or Elusive Species: The Illusion of Reality and a Call for Evidentiary Standards. *BioScience*, 58(6), 549–555. <https://doi.org/10.1641/B580611>
- Msoffe, F., Mturi, F. A., Galanti, V., Tosi, W., Wauters, L. A., & Tosi, G. (2007). Comparing data of different survey methods for sustainable wildlife management in hunting areas: The case of Tarangire–Manyara ecosystem, northern Tanzania. *European Journal of Wildlife Research*, 53(2), 112–124. <https://doi.org/10.1007/s10344-006-0078-7>
- Obura, D. O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoily, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M., & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, 373(6556), 746–748. <https://doi.org/10.1126/science.abh2234>
- O’Connell, A. F., Nichols, J. D., Karanth, K. U., & Royle, J. A. (2011). Camera trap in Ecology. In *Camera Traps in Animal Ecology* (pp. 163–190). Springer Japan. [https://doi.org/10.1007/978-4-431-99495-4\\_10](https://doi.org/10.1007/978-4-431-99495-4_10)
- Osner, N. (2022). *TrapTagger* [Computer software]. <https://github.com/WildEyeConservation/TrapTagger>
- Pardo, L. E., Bombaci, S. P., Huebner, S., Somers, M. J., Fritz, H., Downs, C., Guthmann, A., Hetem, R. S., Keith, M., le Roux, A., Mgqatsa, N., Packer, C., Palmer, M. S., Parker, D. M., Peel, M., Slotow, R., Strauss, W. M., Swanepoel, L., Tambling, C., ... Venter, J. A. (2021). Snapshot Safari: A large-scale collaborative to monitor Africa’s remarkable biodiversity. *South African Journal of Science*, 117(1/2). <https://doi.org/10.17159/sajs.2021/8134>
- Parsons, A. W., Bland, C., Forrester, T., Baker-Whetton, M. C., Schuttler, S. G., McShea, W. J., Costello, R., & Kays, R. (2016). The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. *Biological Conservation*, 203, 75–88. <https://doi.org/10.1016/j.biocon.2016.09.001>
- Pearse, A. T., Krapu, G. L., Brandt, D. A., & Sargeant, G. A. (2015). Timing of spring surveys for midcontinent sandhill cranes: Crane Survey Timing. *Wildlife Society Bulletin*, 39(1), 87–93. <https://doi.org/10.1002/wsb.496>
- Pédarros, É., Coetsee, T., Fritz, H., & Guébois, C. (2020). Rallying citizen knowledge to assess wildlife occurrence and habitat suitability in anthropogenic landscapes. *Biological Conservation*, 242, 108407. <https://doi.org/10.1016/j.biocon.2020.108407>
- Petracca, L. S., & Frair, J. L. (2017). When methodological flaws limit inference: A response to Caruso et al. *Oryx*, 51(2), 208–208. <https://doi.org/10.1017/S0030605316000788>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Roux, Dirk J., M. Kyle S. Smith, Izak P. J. Smit, Stefanie Freitag, Liandi Slabbert, Mohlamatsane M. Mokhatla, Jessica Hayes, et Nelsiwe P. Mpapane. (2020) Cultural Ecosystem Services as Complex Outcomes of People–Nature Interactions in Protected Areas. *Ecosystem Services* 43. <https://doi.org/10.1016/j.ecoser.2020.101111>.
- SANParks. (2020). *Garden Route National Park: Park Management Plan For the period 2020—2029*. Pretoria: Department of Environment, Forestry and Fisheries.
- Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., & Ancillotto, L. (2019). One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology Letters*, 22(2), 365–376. <https://doi.org/10.1111/ele.13199>

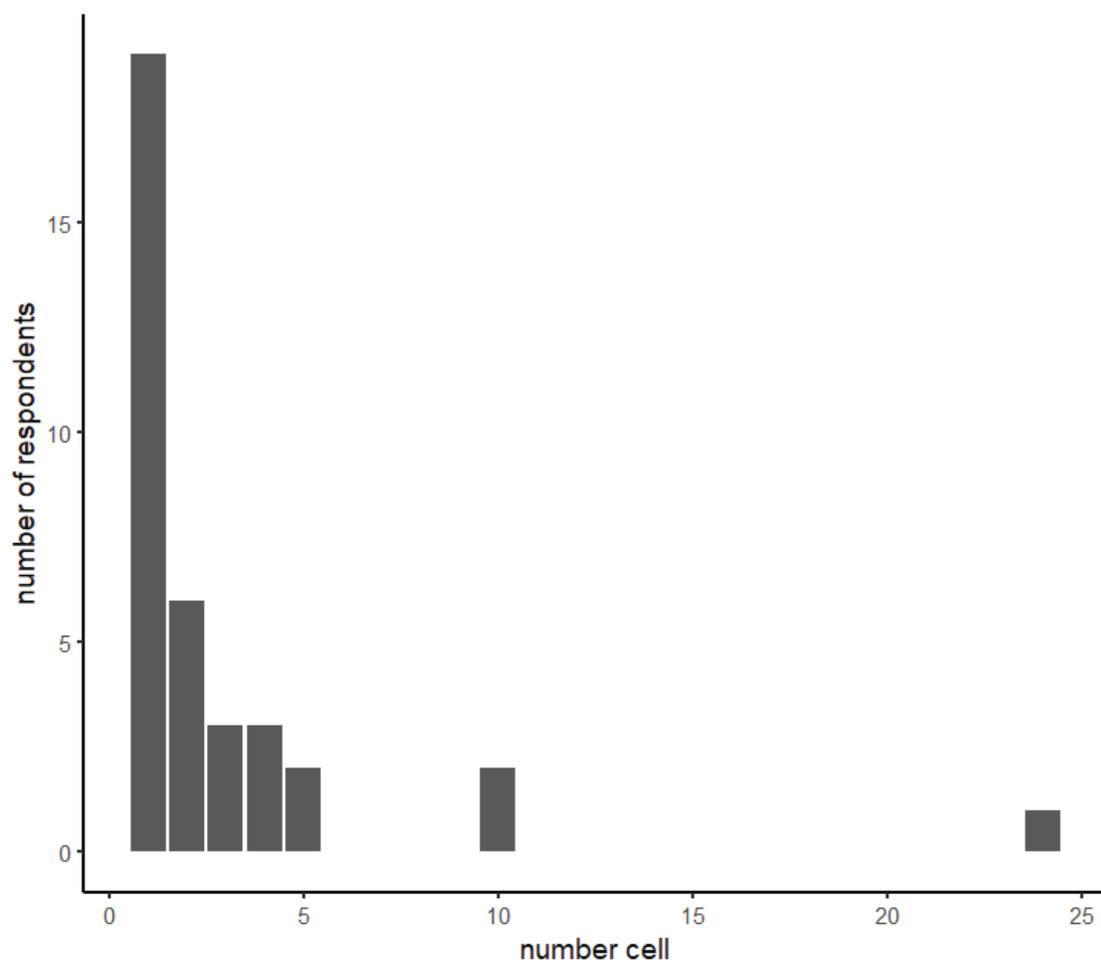
- Schaller, N., Lazrak, E. G., Martin, P., Mari, J.-F., Aubry, C., & Benoît, M. (2012). Combining farmers' decision rules and landscape stochastic regularities for landscape modelling. *Landscape Ecology*, 27(3), 433–446. <https://doi.org/10.1007/s10980-011-9691-2>
- Service, C. N., Adams, M. S., Artelle, K. A., Paquet, P., Grant, L. V., & Darimont, C. T. (2014). Indigenous Knowledge and Science Unite to Reveal Spatial and Temporal Dimensions of Distributional Shift in Wildlife of Conservation Concern. *PLOS ONE*, 9(7), e101595. <https://doi.org/10.1371/journal.pone.0101595>
- Seymour, C. L., Simmons, R. E., Morling, F., George, S. T., Peters, K., & O'Riain, M. J. (2020). Caught on camera: The impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. *Global Ecology and Conservation*, 23, e01198. <https://doi.org/10.1016/j.gecco.2020.e01198>
- Sollmann, R., Mohamed, A., Samejima, H., & Wilting, A. (2013). Risky business or simple solution – Relative abundance indices from camera-trapping. *Biological Conservation*, 159, 405–412. <https://doi.org/10.1016/j.biocon.2012.12.025>
- Swan, M., Di Stefano, J., Christie, F., Steel, E., & York, A. (2014). Detecting mammals in heterogeneous landscapes: Implications for biodiversity monitoring and management. *Biodiversity and Conservation*, 23(2), 343–355. <https://doi.org/10.1007/s10531-013-0604-3>
- Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., ... Zi, F. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 6374, 6. <https://doi.org/10.1126/science.aam9712>
- Turvey, S. T., Risley, C. L., Moore, J. E., Barrett, L. A., Yujiang, H., Xiujiang, Z., Kaiya, Z., & Ding, W. (2013). Can local ecological knowledge be used to assess status and extinction drivers in a threatened freshwater cetacean? *Biological Conservation*, 157, 352–360. <https://doi.org/10.1016/j.biocon.2012.07.016>
- UNEP-WCMC, IUCN, & NGS. (2020). Protected Planet Report 2020. Cambridge UK; Gland, Switzerland; and Washington, D.C., USA. <https://livereport.protectedplanet.net>
- Venables, W., & Ripley, B. (2002). *Modern Applied Statistics with S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0, <https://www.stats.ox.ac.uk/pub/MASS4/>.
- Western Cape Government. (2019). Socio-economic profile: Garden Route District Municipality. <https://www.westerncape.gov.za/provincial-treasury/files/atoms/files/SEP-LG%202021%20-%20Garden%20Route%20District%20Municipality.pdf>
- White, P. C. L., Jennings, N. V., Renwick, A. R., & Barker, N. H. L. (2005). Questionnaires in ecology: A review of past use and recommendations for best practice. *Journal of Applied Ecology*, 42(3), 421–430. <https://doi.org/10.1111/j.1365-2664.2005.01032.x>
- Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.
- Zwerts, J. A., Stephenson, P. J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P. A., Waarde, J., Sterck, L. E. H. M., Verweij, P. A., Bruce, T., Brittain, S., & Kuijk, M. (2021). Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. *Conservation Science and Practice*, 3(12). <https://doi.org/10.1111/csp2.568>

**Supplementary material for the manuscript 4: Comparing local ecological knowledge and with camera trap data to study African mammals' occurrence in anthropogenic landscapes of the Garden Route Biosphere Reserve**

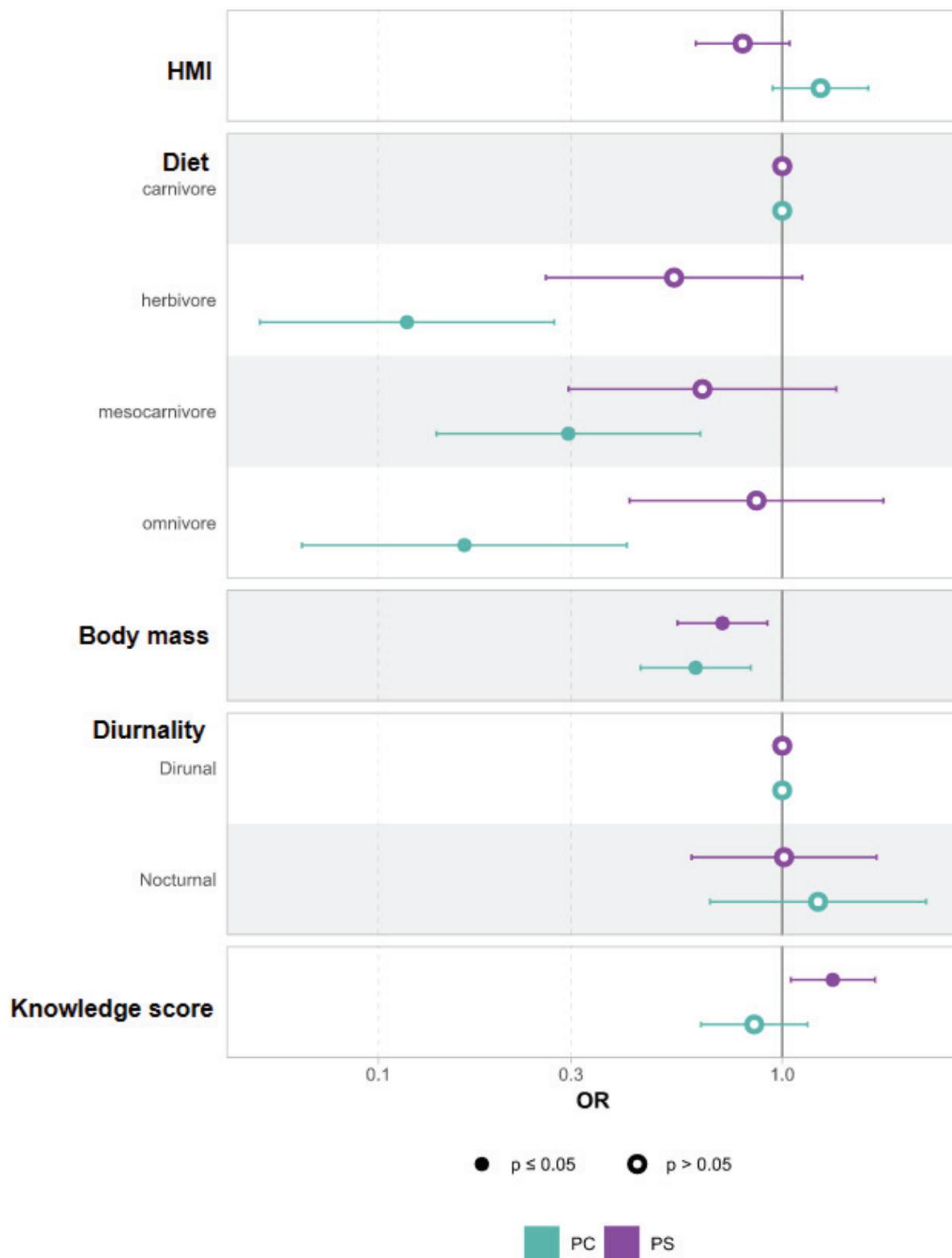
**Figures**



**FIGURE S1** Representation of the value of explicative variable in 2;23\*2;23 km cell.



**FIGURE S2** Representation of the number of survey responses per 2;23\*2;23 km cell.



**FIGURE S3** Outputs of the multinomial model. The odds ratio (OR) for presence on camera only (PC) are represented in blue and presence survey (PS) in purple. A value less than 1 represents a negative effect and a value greater than 1 a positive effect on the probability of detection.

## Tables

**TABLE S1** Summary table of the detection results for the 16 species on the 35 common cells.

English name	Scientific name	IUCN	Percentage of cell occupied according to the survey (%)	Percentage of cell occupied according to CTs (%)
Bushbuck	<i>Tragelaphus scriptus</i>	LC	97	97
South African large-spotted genet	<i>Genetta tigrina</i>	LC	43	97
Bushpig	<i>Potamochoerus larvatus</i>	LC	86	83
Cape porcupine	<i>Hystrix africaeaustralis</i>	LC	94	71
Mongoose: Cape grey mongoose, Large grey mongoose, Water mongoose	<i>Herpestes pulverulentus</i> , <i>Herpestes ichneumon</i> , <i>Atilax paludinosus</i>	LC	77	69
Leopard	<i>Panthera pardus</i>	VU	23	63
Chacma baboon	<i>Papio ursinus ursinus</i>	LC	69	60
Honey badger	<i>Mellivora capensis</i>	LC	43	60
Caracal	<i>Caracal caracal</i>	LC	71	54
Vervet monkey	<i>Cercopithecus pygerythrus</i>	LC	71	43
Blue duiker	<i>Philantomba monticola</i>	LC	23	26
Cape grysbok	<i>Raphicerus melanotis</i>	LC	34	11
African clawless otter	<i>Aonyx capensis</i>	NT	23	6
Common duiker	<i>Sylvicapra grimmia</i>	LC	17	0

**TABLE S2** Outputs of the multinomial model. OR = Odds Ratio and CI= Confidence Interval

<b>Characteristic</b>	<b>OR</b>	<b>95% CI</b>	<b>p-value</b>
<b>PC</b>			
<b>HMI</b>	1.24	0.95, 1.64	0.12
<b>Diet</b>			
<i>carnivore</i>	—	—	
<i>herbivore</i>	0.12	0.05, 0.27	<0.001
<i>mesocarnivore</i>	0.30	0.14, 0.63	0.001
<i>omnivore</i>	0.16	0.06, 0.41	<0.001
<b>Body_mass</b>	0.61	0.45, 0.84	0.002
<b>Diurnality</b>			
<i>Diurnal</i>	—	—	
<i>Nocturnal</i>	1.23	0.66, 2.27	0.5
<b>Knowledge_score</b>	0.85	0.63, 1.15	0.3
<b>PS</b>			
<b>HMI</b>	0.80	0.61, 1.04	0.10
<b>Diet</b>			
<i>carnivore</i>	—	—	
<i>herbivore</i>	0.54	0.26, 1.12	0.10
<i>mesocarnivore</i>	0.63	0.30, 1.36	0.2
<i>omnivore</i>	0.86	0.42, 1.78	0.7
<b>Body_mass</b>	0.71	0.55, 0.92	0.009
<b>Diurnality</b>			
<i>Diurnal</i>	—	—	
<i>Nocturnal</i>	1.01	0.60, 1.71	>0.9
<b>Knowledge_score</b>	1.33	1.05, 1.70	0.019

## Manuscript 5

### Combining local ecological knowledge with camera traps to assess the link between African mammal life history traits and their use of anthropogenic landscapes

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## Abstract

Transformations of natural landscapes often lead to homogenization of wildlife communities, where only the ones capable to adapt are present. Understanding what influences species composition is crucial to predict the destabilization of communities induced by land transformation. In this study, conducted in the Garden Route Biosphere Reserve, South Africa, we explored how mammal species' life history traits influence their capacity to cope with human-dominated habitats testing gradient of anthropogenic transformation (human modification index and cultivated areas), and of naturalness (natural and protected areas). We compared species composition based on life history traits relative to diet and biodemographic strategy using occurrence data combined from camera trapping and local ecological knowledge survey. Our results confirmed that the occurrence of mammals in human-modified habitats was associated with specific traits. Areas highly modified by humans were more favorable for generalist species than for strict carnivores and were mostly used by smaller species. Natural and protected areas did not select for any traits, supporting their role of refugia areas for all wildlife species. Cultivated areas also did not select for a specific trait. The landscape features did not select a reproduction strategy, such as fast versus slow reproduction as expected. Combining monitoring methods enabled to increase the spatial coverage and sample size, and involve various stakeholders in the scientific process. We provided valuable insights to document how human-dominated landscapes affect mammal communities that could be used to design wildlife-friendly anthropogenic spaces for coexistence.

**Key words:** Wildlife monitoring, participatory research, habitat transformation, mammal ecology, diet diversity, r/K strategy, human-wildlife coexistence, conservation, biosphere reserve

## 1 | Introduction

Humans footprint, a measure of the impact of humans on terrestrial land has increase worldwide across the last decades (Venter et al., 2016), thus creating novel environments which are confronting wildlife to conditions usually not encountered in natural environments (Fleming & Bateman, 2018). Human-dominated habitats regroup new land-uses, the presence of roads, buildings, as well as increased urban noises or artificial light, which affect wildlife occurrence (Fleming & Bateman, 2018). Indeed, it has been shown that human practices and activities along an urban-natural gradient often negatively affect species (Hulme-Beaman et al., 2016; McKinney, 2002). This can disrupt the functioning of communities (Wang et al., 2015), as human-modified environments create new niche partitioning and potentially new competition between species (Sévêque et al., 2020; Van Scoyoc et al., 2023). These modifications can eventually lead to local extinction of species (Grimm et al., 2008) as well as local overabundance (Pocock et al., 2004; Stenseth et al., 2003). Globally, species' community composition in such environments tends to homogenize (Newbold et al., 2018), towards species often called 'winners', i.e., able to adjust to new conditions (Grimm et al., 2008). These 'winners' species do well and even better in these new environments (Barrett et al., 2019; Fleming & Bateman, 2018). Anthropogenic landscapes and urban habitats can benefit certain wild mammals (Santini et al., 2019), such as some mesocarnivores species (Louvrier et al., 2021; Wang et al., 2015). Human-dominated habitats, can offer wildlife new resources such as pets, livestock or human commensal species, on which carnivores can predate (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016). Anthropogenic areas could concentrate prey around waterholes or artificial lighting, thus reducing foraging cost of predators (Fleming & Bateman, 2018). The novel environments can be the ground for the development of new techniques to find easily accessible food and some species will, for example, start to steal food from human houses (Hoffman & O'Riain, 2012; Mazue et al., 2023). Commensal species, defined as those benefiting from another species without having any incidence on this species, such as rodents, can often be considered invasive species because of their high capacity to colonize, adapt and occupy new locations (Hulme-Beaman et al., 2016). In the context of globalized transformation of the terrestrial land by humans and their activities, it is necessary to understand the traits which could enable species to successfully use anthropogenic matrices. Studying such traits will help understanding the community that will be maintained in such environments (Hulme-Beaman et al., 2016). Mammals are a good model to study the effect of traits on their capacity to use anthropogenic environments as they represent a diversity of size, diet and ecological requirements (Santini et al., 2019), as well as a recreational attraction (Okello et al., 2008) and subjects of tension with humans (Kansky & Knight, 2014).

Several studies showed that life history traits determine species capacity to adjust to a new environment, which seems to depend on the taxon and the population considered (Hulme-Beaman et al., 2016; Santini et al., 2019). Traits could explain species sensitivity to human disturbances such as human presence or footprint (Lovell et al., 2022; Suraci et al., 2021). By repeatedly facing negative situations with humans, some species can learn and modify their behavior to avoid conflictual situations (Barrett et al., 2019). The demographic traits of adaptable species are often considered to belong to the r-strategy (high fecundity, large litter size) (Hulme-Beaman et al., 2016), as they respond quickly to favorable conditions. Species

considered invasive often breed rapidly, do not live long, and can live at high density (Hulme-Beaman et al., 2016; Pocock et al., 2004). Species with plasticity in feeding behavior, diet (generalist or omnivorous habits) or habitats they occupy are also more likely to adapt and benefit from these new environments (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016). Conversely, species with high space requirements, *i.e.* those most negatively impacted by habitat loss and fragmentation, are expected not to adapt well (Tucker et al., 2018). Solitary species, *i.e.* those that usually do not live at high density, are unlikely to perform well in anthropogenic environments (Hulme-Beaman et al., 2016). Wang et al. (2015) showed that the occupancy of puma (*Puma concolor*), a large solitary carnivore, was lower in high residential areas. Conversely, large carnivores, such as leopard (*Panthera pardus*), have been shown to perform well in the vicinity of humans (Athreya et al., 2013), suggesting that the patterns are not that simple. Ability to adapt to new environments could also be made possible by other factors than life-history traits such as cognitive capacities that benefit the species (Barrett et al., 2019).

Several methods to monitor mammal communities can potentially be used and combined (**manuscript 4**). Interview data have been compared to camera traps (CTs) data, to account for potential bias (Burt et al., 2021; Martínez-Martí et al., 2016). Combining methods provides complementary information mutually improves the understanding of phenomena while increasing the spatial coverage and number of responses (Schaller et al., 2012; Service et al., 2014). In this study we used the complementarity of CTs and local ecological knowledge (LEK) to explore how life history traits influence wild mammal occurrence in the anthropogenic multifunctional landscapes of the Garden Route Biosphere Reserve (GRBR) in South Africa. We studied life history traits relative to diet (type and diversity of resources consumed) and r/K strategy (longevity, gestation length, age at sexual maturity and litter size, body mass). We expected species with a more generalist diet to be attracted to human-dominated habitats because of the easy food resources available while avoiding human encounters to limit negative experiences (Hulme-Beaman et al., 2016). Large and strictly carnivorous species should avoid human-occupied areas, which should favor the presence of smaller carnivores and herbivores in the vicinity of humans (Berger, 2007; Suraci et al., 2021). Species with long generation lengths (slow reproduction parameters) and large body mass should avoid modified landscapes where adult mortality is highest and be found in natural habitats and less disturbed areas, probably also showing a dependence on natural corridors (Brennan et al., 2022; Santini et al., 2019).

## 2 | Materials and methods

### 2.1 | Study area

Our study took place in the GRBR in the Western Cape, on the south-eastern coast of South Africa, between the Indian Ocean and the Outeniqua mountains (Figure 1). Human-transformed landscapes are associated with multiple land-uses such as exotic tree plantations, crop and dairy farming, urban and peri-urban developments, and a vast road network (Baard et al., 2015; SANParks, 2020). The Garden Route National Park (GRNP) is an unfenced protected area managed by South African National Parks with the primary objective of protecting the endemic indigenous forest but also the lakes and wetlands of the area. Other

types of natural vegetation can be found in the GRBR such as fynbos and thicket (Baard et al., 2015).

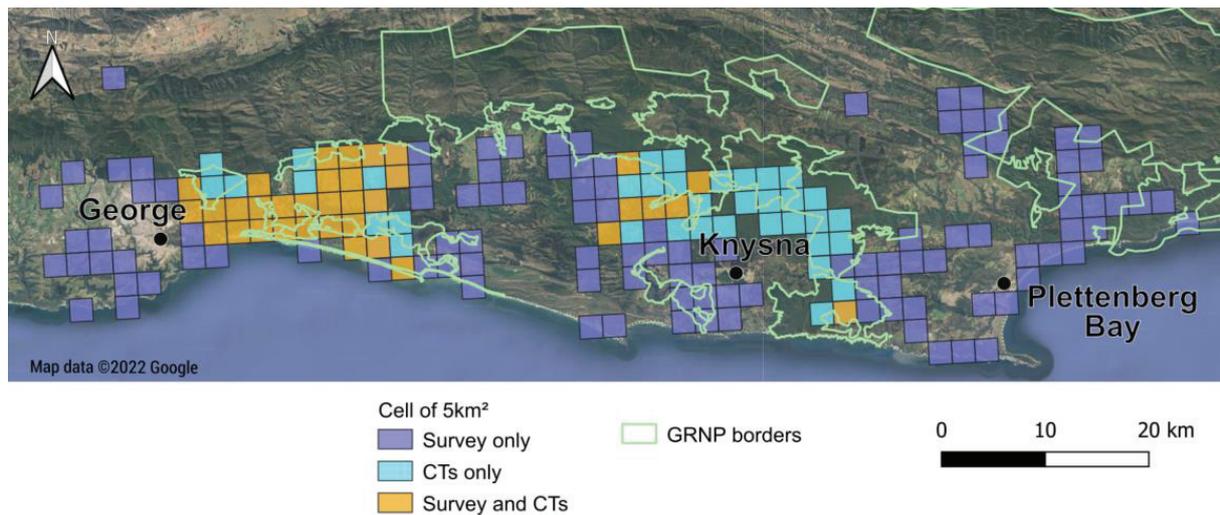
## 2.2 | Data collection

### 2.2.1 | Camera traps

We set-up 75 CTs: 30 cameras were set-up in the GRNP, the rest (45 cameras) were set-up in human-dominated areas (Figure 1). We deployed two models of CTs: 33 Bushnell Trophy Cam HD Aggressor and 41 SPYPOINT Force Dark. As contributing to the Snapshot Safari Project (Pardo et al., 2021), each CT was positioned to detect medium to large mammals as close as possible to the center of a regular grid of 2.23\*2.23 km, 50 cm above the ground, mainly on trees (**manuscript 1**). Each camera was programmed to take a series of three images within 1–5 seconds of each other. CTs were checked every two to three months to change the batteries and SD cards. The data used in this study were produced from a survey running from the 2<sup>nd</sup> of February 2021 to the 20<sup>th</sup> of May 2022, and four cameras were stolen during this period.

### 2.2.2 | Online survey

We used a participatory approach and designed an online survey questionnaire to gain more knowledge on species occupying human-dominated landscapes (Appendix 1). The survey targeted landowners of the GRBR. Once finalized through piloting and revisions, the survey was sent using mailing lists obtained thanks to CapeNature, SANParks, Wildlife and Environment Society of South Africa, local conservancies, WhatsApp and Facebook groups. We also published the link to the survey in local newspapers (George Herald's, The Edge). This research was approved by the Nelson Mandela University ethics committee (H20-SCI-SRU-002). Participants indicated on a cell of 2.23\*2.23 km on a map the location of their property, no exact global positioning system (GPS) location had to be shared, thus preserving the anonymity of the participants (Figure 1), corresponding to the CTs grid. The survey was available in English and Afrikaans, and was accessible online from November 2021 to March 2022. Species presence was assessed by a question on the frequency to which the respondent saw the species on their properties. They had multiple choices for the species and the frequency of sightings (not anymore, rarely, occasionally, frequently, very frequently). Respondents could select generic categories for 'mongoose' or 'genet' when they did not know the differences between the species in these two taxonomic groups. The ecological knowledge of the respondents was tested by asking four questions in the survey. Two were based on identifying a species using a photograph: a herbivore (blue duiker; *Philantomba monticola*) and mesocarnivore (Cape grey mongoose *Herpestes pulverulentus*). The third required respondents to identify the track of a carnivore (caracal, *Caracal caracal*), and the fourth to identify the scat of a herbivore (porcupine, *Hystrix africaeaeaustralis*). For each question, respondents were given a choice of three species. They also indicated their main activities, involvement in conservation initiatives and other information about them and their properties. A more detailed description can be found in the **manuscript 2** of this *PhD* thesis.



**FIGURE 1** Study area in Garden Route Biosphere Reserve, South Africa. The grid cells represent the 5 km<sup>2</sup> cells, colored by the type of data available: in purple survey only, in blue CTs only and in orange survey and CTs data were available. We plotted the borders of the Garden Route National Park in light green.

## 2.3 | Data processing

### 2.3.1 | Estimating wildlife occurrence

#### 2.3.1.1 | From camera traps

The photographs were manually tagged, firstly by using digiKam (digikam team, 2001), then with the online software TrapTagger (Osner, 2022). All species detected were tagged but for this analysis, we focused on mammal species >500 g and all the other photographs were not considered. We filtered the data to keep only one photograph every 30 min for a given species to ensure independent events. When the species was detected at least one time it was classified as 'present' and it was considered 'absent' otherwise.

#### 2.3.1.2 | From online survey

Respondents indicated the frequency at which they detected each species and we transformed this frequency of occurrence to obtain a presence/absence variable. When a respondent did not tick a species or reported that a species no longer occurred on their property, we assigned the variable a value of 0 (absence). When a species occurred very frequently or frequently, we assigned the value of 3 (the two categories were grouped), occasionally was assigned a value of 2 and rarely of 1. We averaged the frequency of occurrence for each species on each cell, and considered the species was present if the score was equal or above 1 and assigned a value of 1 for all presence. Because mongooses and genets were difficult to distinguish, we used the general categories 'mongooses' (including the Cape grey mongoose, large grey mongoose and water mongoose) and 'genets' (including the large-spotted genet and small-spotted genet) in subsequent analyses. Only the large-spotted genet has been recently recorded in the area and detected with the CTs, although both species are listed as potentially occurring (Baard et al. 2015). Therefore, we considered the responses to refer to the large-spotted genet. As there was too much uncertainty regarding mongooses' identification during the survey, the three species were excluded from the analyses testing trait-presence

relationships (**manuscript 4**). However, they were kept to describe the overall range of species traits in our study area.

### 2.3.1.3 | Combining datasets

To get more robust survey data, we compiled the average detection frequency per cell. We only keep average values above one, *i.e.* than the species detected more than 'rarely', to have more confidence in the reported presence of a species. When the average value was above one, we transformed it as a 1 for presence, and values under 1, were considered as absence (0). To further assess the reliability of the survey data, we calculated each respondent's naturalist score by calculating their score at the knowledge questions and we averaged the knowledge score of all the respondents of the same cell. We obtained a variable between 0%, when all the respondents were wrong to each question and 100%, when they responded correctly to all questions. For carnivores and mesocarnivores, as they were species with lower match between CTs and survey, when only one person responded in a cell, we only kept data for people with a knowledge score above 50% (**manuscript 4**). We then combined the presence and absence from the survey, to one of the CTs, to increase our spatial coverage. In cells where only CTs were present, we coded presence and absence following the species detected by the CTs. When a cell had information from the CTs and the survey, if the CTs detected the species, we considered the species was present on the cell (1). If the CTs did not detect the species, we evaluated the presence thanks to the survey, if the survey indicated a presence, we changed the value to 1 for the couple species-cell, if the species was absent we used the value 0. For each cell and species, we got presence and absence data.

### 2.3.2 | Describing anthropogenic transformations in the landscape

To assess environmental conditions, we calculated variables to characterize anthropogenic landscapes at the scale of the 2.23\*2.23km cell. Using a shapefile from SANParks (Baard et al., 2015), that we rasterized on QGIS, we calculated the percentage of protected areas in each cell. We calculated the proportion of forest, fynbos, thicket and wetland in each cell, by summing the number of pixel from each land cover ("aggregate" function, "stats" package), using the 2020 SA National Land Cover Datasets (Department of Forestry, Fisheries and the Environment, 2020). We then summed all the previously cited land cover to calculate the proportion of natural habitats in each cell. To obtain a variable describing anthropogenic land cover, we calculated the cultivated areas using the 2020 SA National Land Cover Datasets (Department of Forestry, Fisheries and the Environment, 2020). To test the possible impact of human footprint, we first calculated the mean value of human modification index (HMI) (Kennedy et al., 2020). We then calculated the length of roads in the same cell to assess the potential disturbance associated with human footprint ('st\_intersection' and 'st\_length' function, 'sf' package) (Pebesma, 2018), as density of roads has been shown to affect temporal activity niche of mammals in the GRBR (**manuscript 2**).

### 2.3.3 | Species life history traits

We selected species traits that we expected to affect the probability of presence of mammal species in anthropogenic environments. We used the EltonTraits database (Wilman et al., 2014) to extract data on the diet of each studied species. Following Santini et al. (2019) and Suraci et al. (2021), we calculated the Shannon Index to estimate the dietary diversity for each

species, based on the following diet categories: plants, seeds, fruits, scavenge, other vertebrates, fish, reptiles, mammals/birds and invertebrate (Figure S2). We completed our information using the PanTHERIA database (Jones et al., 2009) to extract traits related to r/K strategy for each species. The traits selected were litter size, length of gestation, age at sexual maturity, longevity and adult body mass (Figure S4 and S5). Species trait values are presented in Table S1.

## 2.3 | Data analyses

### 2.3.1 | Species characterization

We tested the correlation between each variable describing the diet on the one hand and the r/K strategy on the other hand before doing principal components analyses on these traits variables (Figure S1 and S3) ('cor' function, 'stats' package). We used non-highly correlated variables ( $r < 0.7$ ) and removed the variable 'group size' as it was correlated to longevity and age at sexual maturity (Figure S3). We conducted two separated principal components analysis (PCA) one on r/K strategies and one on dietary data ('dudi.pca' function, 'ade4' package) (Dray & Dufour, 2007). We kept the first two axes for the PCA on diet, which accounted for 66.55% of the variation in diet values between species (Figure S2 and Table S1). We extracted the three first axes for the analysis on r/K strategy, which accounted for 90% of the variation values between species (Figure S4 and Table S3). We used these five synthetic variables from these two PCAs to describe species traits to the different anthropogenic variables previously described.

### 2.3.2 | Species responses to anthropogenic variables

We first tested correlations between the five anthropogenic candidate variables described above (proportion of natural habitats, cultivated areas, protected areas, HMI and density of roads) ('cor' function, 'stats' package). Density of roads and HMI value were highly correlated ( $r=0.76$ ), so we decided to keep HMI (Figure S7). When using proportion as variables (protected areas, cultivated areas and protected areas), we used the arcsin-square root transformation classically advised by Sokal and Rohlf (1981). Finally, we scaled the four variables used in the modelling: proportion of natural habitats, cultivated areas, protected areas and HMI ('scale' function), to compare their effect (R Core Team, 2020). For each species, we then ran a generalized linear model ('glm' function) following binomial distribution, using the four non-correlated and scaled variables.

### 2.3.3 | Comparison of the traits selected by anthropogenic pressures

We extracted the estimates from the generalized linear models of the combined survey and CTs presence/absence data of species as a function of anthropogenic attributes: proportion of natural habitats, proportion of protected areas, proportion of cultivated areas and HMI. This provided a set of estimates associated with the probability of presence for a given set of traits corresponding to the different species. We then ran a simple linear model following a normal distribution with estimates associated with the probability of presence against one of the variables describing the traits of the species as an explicative variable. This allowed us to describe the change in the likelihood of presence in the landscape as a function of the trait values.

All the analyses were performed on R (R Core Team, 2020). We used the package “ggplot2” for graphical representation (Wickham, 2016).

### 3 | Results

In total, we used 235 completed surveys and 12,002 independent photographs of wild mammal species, describing 173 cells. Sixteen species were detected combining both methods, although the common duiker (*Sylvicapra grimmia*) was not detected by the CTs (Table 1). The sixteen species included the three species of mongooses, that were not considered in the present analyses, resulting in a total of thirteen species for the trait-presence regression. The bushbuck was the most common species, detected in 75% of the cells, followed by the chacma baboon (64%) and the vervet monkey (63%). The otter (8%), the common duiker (11%) and the blue (12%) duiker were the least widespread.

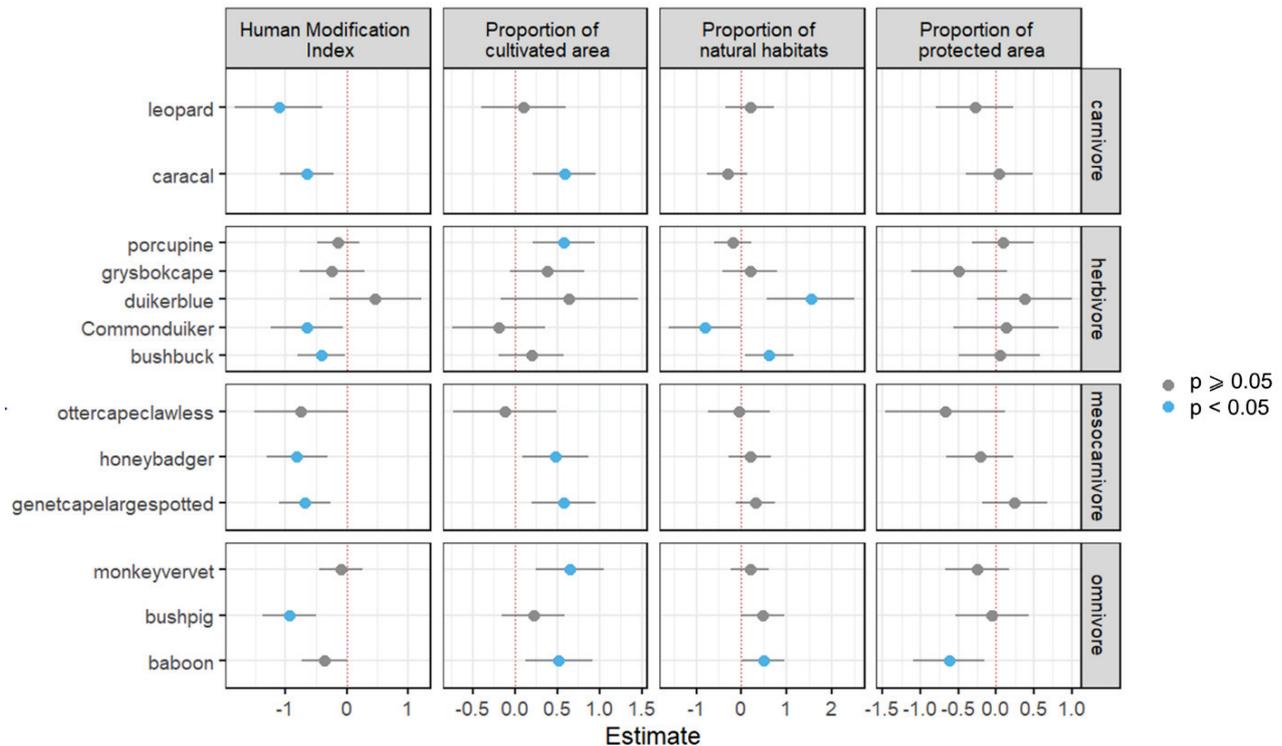
**TABLE 1** Summary table of the detection of 13 species (excluding mongooses).

English name		Scientific name	IUCN	Diet	Percentage of cells where the species was present (%)
Bushbuck		<i>Tragelaphus scriptus</i>	LC	herbivore	75
Chacma baboon		<i>Papio ursinus ursinus</i>	LC	omnivore	64
Vervet monkey		<i>Cercopithecus pygerythrus</i>	LC	omnivore	63
Bushpig		<i>Potamochoerus larvatus</i>	LC	omnivore	58
Cape porcupine		<i>Hystrix africaeaustralis</i>	LC	herbivore	51
South African large-spotted genet		<i>Genetta tigrina</i>	LC	mesocarnivore	52
Caracal		<i>Caracal caracal</i>	LC	carnivore	36
Honey badger		<i>Mellivora capensis</i>	LC	mesocarnivore	31
Cape grysbok		<i>Raphicerus melanotis</i>	LC	herbivore	15
Leopard		<i>Panthera pardus</i>	VU	carnivore	16
Blue duiker		<i>Philantomba monticola</i>	LC	herbivore	12
Common duiker		<i>Sylvicapra grimmia</i>	LC	herbivore	11
African clawless otter		<i>Aonyx capensis</i>	NT	mesocarnivore	8

#### 3.1 | Species responses to anthropogenic variables

We only described significant variables ( $p$ -value  $< 0.05$ ), *i.e.* with tangible effects in the following section (Figure 2, Table S6). Out of 13 species, seven were less detected in areas with more human modification (high HMI): the leopard, caracal, common duiker, bushbuck, honey

badger, genet and bushpig ( $p$ -value  $< 0.05$ , Figure 2). The caracal, porcupine; honey badger, genet, vervet monkey and baboon were more likely to be detected in cells with higher proportion of cultivated areas ( $p$ -value  $< 0.05$ , Figure 2). The blue duiker, bushbuck and baboon were more likely to be detected in areas with higher proportion of natural habitats, whereas the common duiker was less likely to be detected in these habitats ( $p$ -value  $< 0.05$ , Figure 2). Baboon was the only species negatively correlated to higher proportion of protected areas ( $p$ -value  $> 0.05$ , Figure 2).



**FIGURE 2** Estimates from the generalized linear models for each species. Species are sorted by diet type. Significant estimates are represented in blue and non-significant estimates in grey. The grey lines represent the standard deviation multiplied by 1.96. The red lines highlight the position of zero on the x-axis. The further away from zero, the stronger the effect (as variables are scaled). To the right of the lines, species occurrence has a positive relationship to the variable.

### 3.2 | Species traits characterization

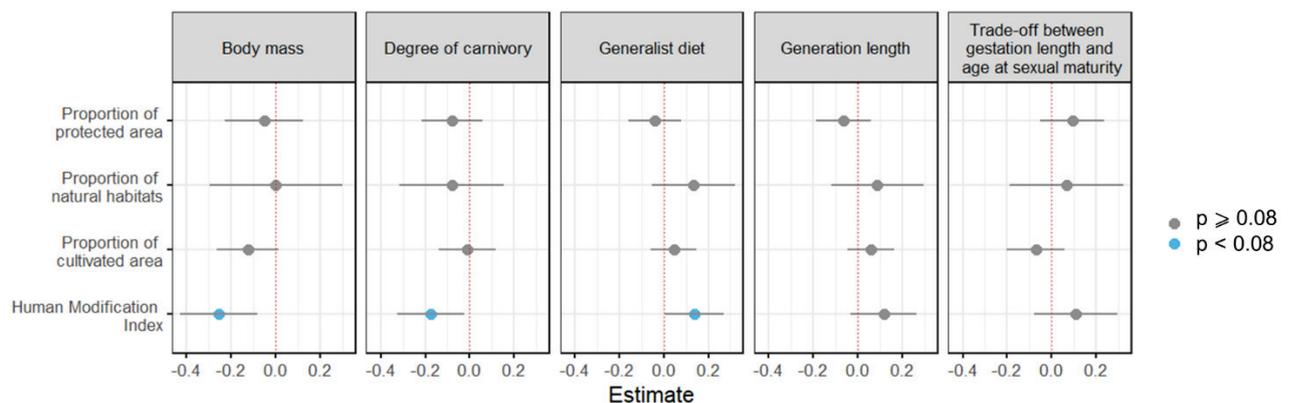
The results of the multivariate analysis on the documented diet of the species present in the GRBR showed that the species were spread along a gradient (1) opposing generalist and specialist species on the first axis, and (2) more carnivorous opposed to herbivorous on the second axis, that we named degree of carnivory (Figure S2, Tables S2 and S3). For the analyses we reversed the first axis of the PCA to describe a gradient called generalist diet (specialist described by negative values and generalist by positive ones).

The results of the multivariate analysis on the  $r/K$  strategy revealed three gradients: (1) species spread along a generation length gradient on the first axis (high longevity, late age at first

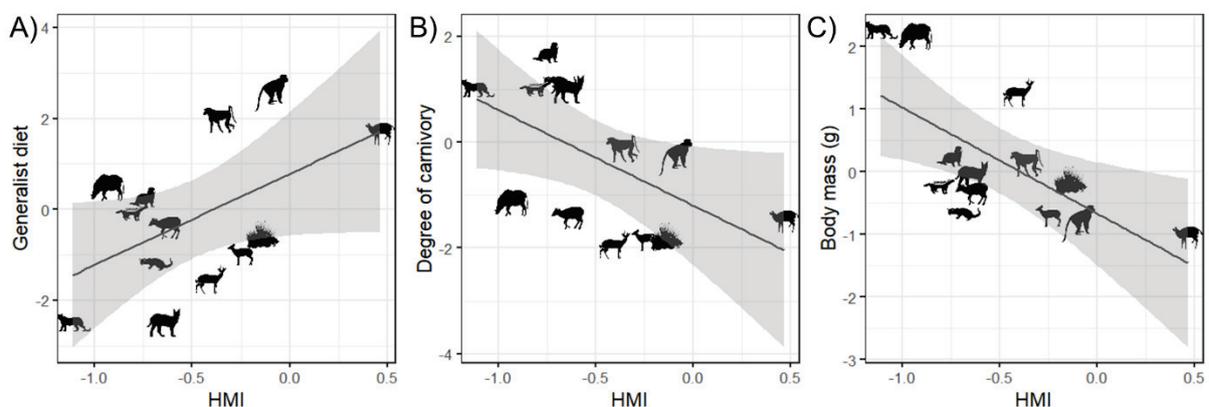
reproduction and long gestation length), opposing species with slow reproduction to those with faster one (also larger litter size), named generation length (Pacifci et al., 2013), (2) the second axis of the PCA separated species with long gestation to those with older age at sexual maturity, that we called trade-off between gestation length and age at sexual maturity, and the third axis described the body mass of the species (Figures S3 and S4, Tables S4 and S5).

### 3.3 | Comparison of the traits selected by anthropogenic pressures

The selection of species traits was only influence by the HMI value (Figure 3, Table S7). The proportion of protected areas, of natural habitats of cultivated areas did not select any trait (Figure 3). Cells with higher values of HMI selected for species with a more generalist diet (Figures 3, and 4A). Increasing values of HMI induced a decrease in the presence probability of strict carnivores and large body mass species (Figures 3, 4B and 4C). Generation length and trade-off between gestation length and age at sexual maturity were not selected (Figure 3).



**FIGURE 3** Estimates from the linear models for each species in function of each species traits. Significant estimates are represented in blue and non-significant estimates in grey. The grey lines represent the standard deviation multiplied by 1.96.



**FIGURE 4** Estimates regarding their response to human modifications (HMI) for each species, represented by its icon, in function of the A) degree of generalist diet, B) degree of carnivory and C) Body mass (g)

body mass The regression line and confidence interval were represented through the 'geom\_smooth' function of ggplot2.

## 4 | Discussion

Combining CTs and LEK data provided reliable information on mammals' use of anthropogenic landscape, while allowing to increase the spatial coverage of our study area to describe the traits allowing mammals to persist in the multifunctional landscape of GRBR. However, we could not use the data on mongooses because of the uncertainty from the survey data (**manuscript 4**). As suggested by Santini et al. (2019), our results supported that anthropogenic landscapes select for specific species life history traits, while a diversity of species were detected across the landscape. This confirms results of other studies on the success of some species, *i.e.* winners, in urban areas (Santini et al., 2019). Mostly diet-related traits played a role in the presence of species in more modified habitats.

Areas highly modified by humans did not favor species with a strict carnivore diet. Few studies suspected that carnivores might take advantage of the commensal species which can be found in anthropogenic landscapes, which did not seem to be the case for the strict carnivores of our study (Fleming & Bateman, 2018; Hulme-Beaman et al., 2016). However, the large-spotted genet was relatively wide spread, in over 50% of the cells, which suggest that this pattern may be mainly driven by large body sized carnivores. It would be interesting to include mongooses, which are flexible small carnivore and may take advantage of anthropogenic environments (Figure S2). Large carnivore species, such as leopards and caracals in our case, probably avoided encountering humans in areas highly used by humans because humans fear them or they can be involved in conflict with humans (Carter & Linnell, 2016; Zimmermann et al., 2020). Avoiding direct encounters might help reducing potential conflicts (Barrett et al., 2019). Species with a generalist diet were more likely to use highly modified areas than the other species. This result was expected, as several studies suggested generalist species could take advantage of the diversity of new resources available such as rubbish or crops (Hulme-Beaman et al., 2016; Santini et al., 2019). The relative absence of large top predators in these highly modified areas could explain why species with less strict carnivore diets (opportunistic mesocarnivores) are favored as they likely benefit from human presence as a shield to avoid predation risk (Berger, 2007). Cells highly modified by humans were mostly used by smaller species. They might perform better in more modified habitats because they can avoid anthropogenic threats (Suraci et al., 2021). Species with higher body mass avoided areas with high HMI values, probably because they need connectivity and are vulnerable to habitat fragmentation (Brennan et al., 2022). Small species could also be more secretive or less scary for people who tolerate them, whereas they do not tolerate larger carnivores (Carter & Linnell, 2016; Treves & Bruskotter, 2014). These results are consistent with what is found in the literature (Oriol-Cotterill et al., 2015; Suraci et al., 2021). In our study, contrary to what was shown in other works, traits related to a fast reproduction strategy did not seem to be favored by areas with higher modification of the landscapes (Santini et al., 2019; Suraci et al., 2021). A reason could be cell's large scale (5 km<sup>2</sup>) or an effect of the mosaic landscapes of the GRBR, which attenuate or render certain effects undetectable. The blue duiker showed a positive although non-significant association with areas with high HMI value, which is surprising considering its

positive association with natural habitats (**manuscripts 2 and 3**). However, it may suggest its capacity to use small patch of natural habitats in human-dominated areas, probably thanks to its small home-range size (Venter et al., 2016; Wilman et al., 2014).

We were surprised to have no traits associated with species using more agricultural areas. We would have expected species with a more flexible and opportunistic diet, such as primates, or species consuming rodents, to take advantage of these areas. Having a generalist diet is a possibly selected trait to take advantage of new food resources (Hulme-Beaman et al., 2016; Santini et al., 2019). Protected areas and natural habitats did not select for a particular type of species, which might be because species, no matter their life-history traits, can occur in these areas, where human perturbations are generally lower. It highlights the importance of protected areas in protecting a diverse community of species in such open multifunctional landscapes. The absence of statistical effects of protected areas could also be explained by the fact that most survey responses were outside protected areas, even if some fell into it (30 cells), and only 30 CTs were in the GRNP, representing 34% of the cells.

Our example of mammal species persistence in multifunctional landscape suggested that human-induced modifications could lead to the selection of specific species traits at a local scale, mostly towards a change of the community structure in favor of smaller and non-strict carnivore, or herbivore, species. The same trend has been described at the scale of the United States of America or even worldwide (Newbold et al., 2018; Santini et al., 2019; Suraci et al., 2021). Diet and biodemographic traits were adequate to predict species persistence and responses in human-dominated landscapes, in particular the body size effect on synanthropy and anthropophoby as defined by Hulme-Beaman et al (2016). Synanthropic species would rather be small species able to mitigate the risk associated with human proximity. Attraction to human-dominated areas and possible resources associated by anthropophilic species seemed to be driven by species with opportunistic omnivore or herbivore diet, which benefit from these cell profiles. We suggest to further investigate the link between behavioral, and even personality traits, and the typology of anthropodependence defined by Hulme-Beaman et al (2016). Our results also concur with other researchers in suggesting that to conserve the largest diversity of species, protected areas and natural habitats need to be preserved within these mosaic landscapes (Obura et al., 2021; Rosenzweig, 2003). The active design of wildlife-friendly spaces, into the anthropogenic matrices could play a major role in conserving biodiversity in modified landscapes, while allowing opportunities for reconnecting people to nature (Obura et al., 2021; Rosenzweig, 2003).

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## References

- Athreya, V., Odden, M., Linnell, J. D. C., Krishnaswamy, J., & Karanth, U. (2013). Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. *PLOS ONE*, 8(3), e57872. <https://doi.org/10.1371/journal.pone.0057872>
- Baard, J., Durrheim, G., Hanekom, N., Hayes, J. S., Kraaij, T., Kruger, N., Ngubeni, N., Randall, R. M., Russell, I. A., Seydack, A. H. W., Smith, K., Van der Vyer, L., & Vermeulen, W. J. (2015). Garden Route National Park—State of knowledge.
- Barrett, L. P., Stanton, L. A., & Benson-Amram, S. (2019). The cognition of ‘nuisance’ species. *Animal Behaviour*, 147, 167–177. <https://doi.org/10.1016/j.anbehav.2018.05.005>
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, 3(6), 620–623. <https://doi.org/10.1098/rsbl.2007.0415>
- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N., & Kremen, C. (2022). Functional connectivity of the world’s protected areas. *Science*, 376(6597), 1101–1104. <https://doi.org/10.1126/science.abl8974>
- Brittain, S., Rowcliffe, M. J., Kentatchime, F., Tudge, S. J., Kamogne-Tagne, C. T., & Milner-Gulland, E. J. (2022). Comparing interview methods with camera trap data to inform occupancy models of hunted mammals in forest habitats. *Conservation Science and Practice*. <https://doi.org/10.1111/csp2.12637>
- Burt, C., Fritz, H., Keith, M., Guerbois, C., & Venter, J. A. (2021). Assessing different methods for measuring mammal diversity in two southern African arid ecosystems. *Mammal Research*, 66(2), 313–326. <https://doi.org/10.1007/s13364-021-00562-x>
- Carter, N. H., & Linnell, J. D. C. (2016). Co-Adaptation Is Key to Coexisting with Large Carnivores. *Trends in Ecology & Evolution*, 31(8), 575–578. <https://doi.org/10.1016/j.tree.2016.05.006>
- Department of Forestry, Fisheries and the Environment. (2020). South African National Landcover Data. [https://egis.environment.gov.za/sa\\_national\\_land\\_cover\\_datasets](https://egis.environment.gov.za/sa_national_land_cover_datasets)
- digikam team. (2001). DigiKam [Computer software]. <https://www.digikam.org/>
- Dray, S., & Dufour, A. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, 22(4), 1–20. <https://doi.org/10.18637/jss.v022.i04>
- Fleming, P. A., & Bateman, P. W. (2018). Novel predation opportunities in anthropogenic landscapes. *Animal Behaviour*, 138, 145–155. <https://doi.org/10.1016/j.anbehav.2018.02.011>
- Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global Change and the Ecology of Cities. *Science*, 319(5864), 756–760. <https://doi.org/10.1126/science.1150195>

- Hoffman, T. S., & O’Riain, M. J. (2012). Landscape requirements of a primate population in a human-dominated environment. *Frontiers in Zoology*, 9(1), 1. <https://doi.org/10.1186/1742-9994-9-1>
- Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, 31(8), 633–645. <https://doi.org/10.1016/j.tree.2016.05.001>
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O’Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90(9), 2648–2648. <https://doi.org/10.1890/08-1494.1>
- Kansky, R., & Knight, A. T. (2014). Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation*, 179, 93–105. <https://doi.org/10.1016/j.biocon.2014.09.008>
- Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2020). Global Human Modification of Terrestrial Systems. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/edbc-3z60>
- Louvrier, J. L. P., Planillo, A., Stillfried, M., Hagen, R., Börner, K., Kimmig, S., Ortmann, S., Schumann, A., Brandt, M., & Kramer-Schadt, S. (2021). Spatiotemporal interactions of a novel mesocarnivore community in an urban environment before and during SARS-CoV-2 lockdown. *Journal of Animal Ecology*, n/a(n/a). <https://doi.org/10.1111/1365-2656.13635>
- Lovell, C., Li, S., Turner, J., & Carbone, C. (2022). The effect of habitat and human disturbance on the spatiotemporal activity of two urban carnivores: The results of an intensive camera trap study. *Ecology and Evolution*, 12(3), e8746. <https://doi.org/10.1002/ece3.8746>
- Martínez-Martí, C., Jiménez-Franco, M. V., Royle, J. A., Palazón, J. A., & Calvo, J. F. (2016). Integrating occurrence and detectability patterns based on interview data: A case study for threatened mammals in Equatorial Guinea. *Scientific Reports*, 6(1), 33838. <https://doi.org/10.1038/srep33838>
- Mazue, F., Guerbois, C., Fritz, H., Rebut, N., & Petit, O. (2023). Less bins, less baboons: Reducing access to anthropogenic food effectively decreases the urban foraging behavior of a troop of chacma baboons (*Papio hamadryas ursinus*) in a peri-urban area. *Primates*, 64, 91–103. <https://doi.org/10.1007/s10329-022-01032-x>
- McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*, 52(10), 883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- Newbold, T., Hudson, L. N., Contu, S., Hill, S. L. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R. P., Scharlemann, J. P. W., & Purvis, A. (2018). Widespread winners and narrow-ranged losers:

Land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, 16(12), e2006841. <https://doi.org/10.1371/journal.pbio.2006841>

Obura, D. O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoily, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M., & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, 373(6556), 746–748. <https://doi.org/10.1126/science.abh2234>

Okello, M. M., Manka, S. G., & D'Amour, D. E. (2008). The relative importance of large mammal species for tourism in Amboseli National Park, Kenya. *Tourism Management*, 29(4), 751–760. <https://doi.org/10.1016/j.tourman.2007.08.003>

Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C., & Macdonald, D. W. (2015). Landscapes of Coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, 124(10), 1263–1273. <https://doi.org/10.1111/oik.02224>

Osner, N. (2022). TrapTagger [Computer software]. <https://github.com/WildEyeConservation/TrapTagger>

Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P., & Rondinini, C. (2013). Generation length for mammals. *Nature Conservation*, 5, 89–94. <https://doi.org/10.3897/natureconservation.5.5734>

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10(1), 439–446. <https://doi.org/10.32614/RJ-2018-009>

Pocock, M. J. O., Searle, J. B., & White, P. C. L. (2004). Adaptations of animals to commensal habitats: Population dynamics of house mice *Mus musculus domesticus* on farms: Population dynamics of commensal house mice. *Journal of Animal Ecology*, 73(5), 878–888. <https://doi.org/10.1111/j.0021-8790.2004.00863.x>

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

Rosenzweig, M. L. (2003). Reconciliation ecology and the future of species diversity. *Oryx*, 37(2), 194–205. <https://doi.org/10.1017/S0030605303000371>

SANParks. (2020). Garden Route National Park: Park Management Plan For the period 2020—2029. Pretoria: Department of Environment, Forestry and Fisheries.

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., & Ancillotto, L. (2019). One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecology Letters*, 22(2), 365–376. <https://doi.org/10.1111/ele.13199>

Schaller, N., Lazrak, E. G., Martin, P., Mari, J.-F., Aubry, C., & Benoît, M. (2012). Combining farmers' decision rules and landscape stochastic regularities for landscape modelling. *Landscape Ecology*, 27(3), 433–446. <https://doi.org/10.1007/s10980-011-9691-2>

- Service, C. N., Adams, M. S., Artelle, K. A., Paquet, P., Grant, L. V., & Darimont, C. T. (2014). Indigenous Knowledge and Science Unite to Reveal Spatial and Temporal Dimensions of Distributional Shift in Wildlife of Conservation Concern. *PLOS ONE*, 9(7), e101595. <https://doi.org/10.1371/journal.pone.0101595>
- Sévêque, A., Gentle, L. K., López-Bao, J. V., Yarnell, R. W., & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95(6), 1689–1705. <https://doi.org/10.1111/brv.12635>
- Sokal, R. R., & Rohlf, F. J. (1981). *Biometry*. W. H. Freeman, San Francisco.
- Stenseth, N. C., Leirs, H., Skonhøft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Singleton, G. R., Lima, M., Machang'u, R. S., Makundi, R. H., Zhang, Z., Brown, P. R., Shi, D., & Wan, X. (2003). Mice, rats, and people: The bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, 1(7), 367–375. [https://doi.org/10.1890/1540-9295\(2003\)001\[0367:MRAPTBJ2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0367:MRAPTBJ2.0.CO;2)
- Suraci, J. P., Gaynor, K. M., Allen, M. L., Alexander, P., Brashares, J. S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L. M., Forrester, T., Green, A. M., Haight, J., Harris, N. C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P. E., Lewis, J. S., McInturff, A., ... Wilmers, C. C. (2021). Disturbance type and species life history predict mammal responses to humans. *Global Change Biology*, 27(16), 3718–3731. <https://doi.org/10.1111/gcb.15650>
- Treves, A., & Bruskotter, J. (2014). Tolerance for Predatory Wildlife. *Science*, 344(6183), 476–477. <https://doi.org/10.1126/science.1252690>
- Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Moorther, B. V., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., ... Zi, F. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 6374, 6. <https://doi.org/10.1126/science.aam9712>
- Van Scoyoc, A., Smith, J. A., Gaynor, K. M., Barker, K., & Brashares, J. S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, 1365-2656.13892. <https://doi.org/10.1111/1365-2656.13892>
- Venter, J., Seydack, A., Ehlers Smith, Y., Uys, R., & Child, M. F. (2016). A conservation assessment of *Philantomba monticola*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa. 9.
- Venter, O., Sanderson, E. W., Magrath, A., Allan, J. R., Beher, J., Jones, K. R., Possingham, H. P., Laurance, W. F., Wood, P., Fekete, B. M., Levy, M. A., & Watson, J. E. M. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, 7(1), 12558. <https://doi.org/10.1038/ncomms12558>

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation*, 190, 23–33. <https://doi.org/10.1016/j.biocon.2015.05.007>

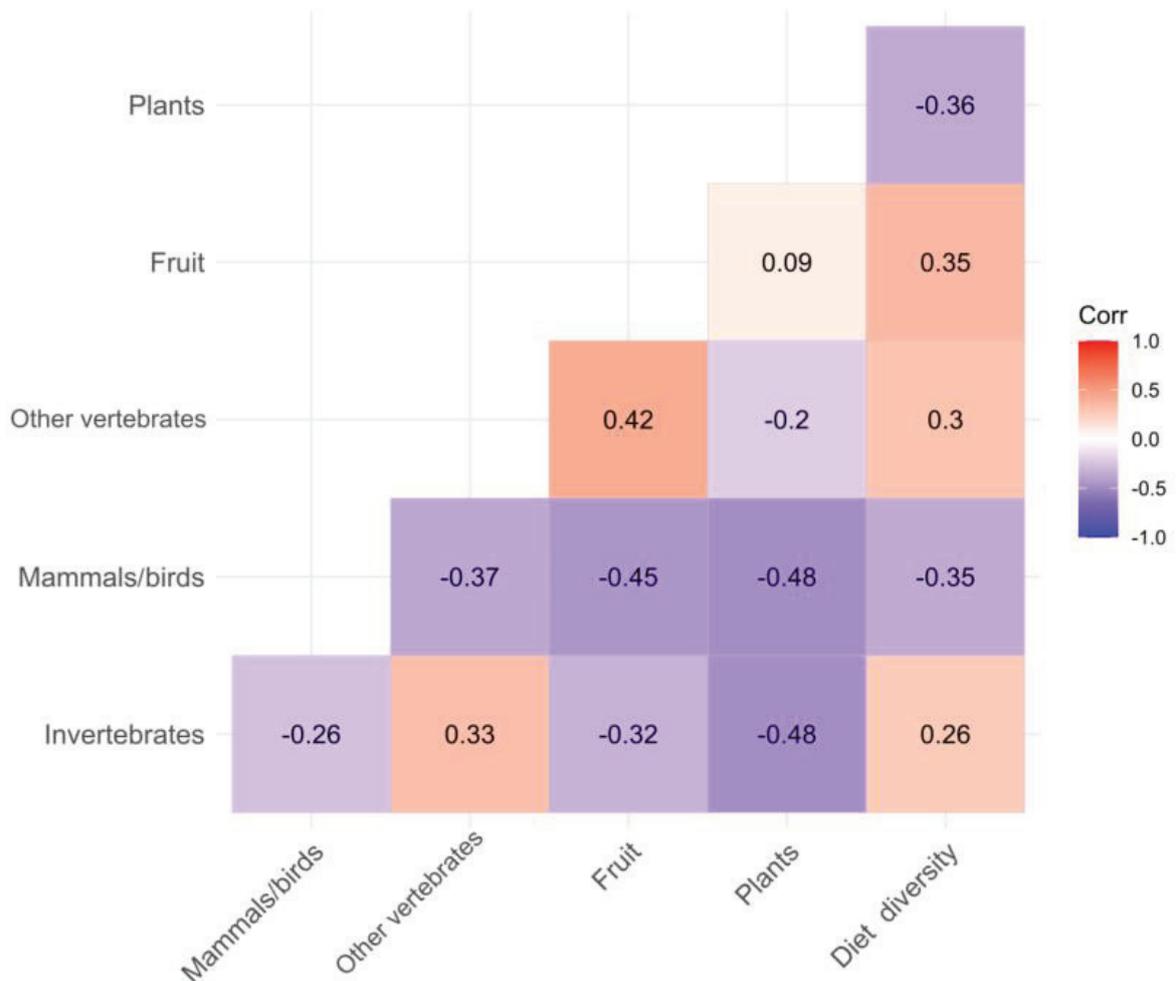
Wickham, H. (2016). *Ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(7), 2027–2027. <https://doi.org/10.1890/13-1917.1>

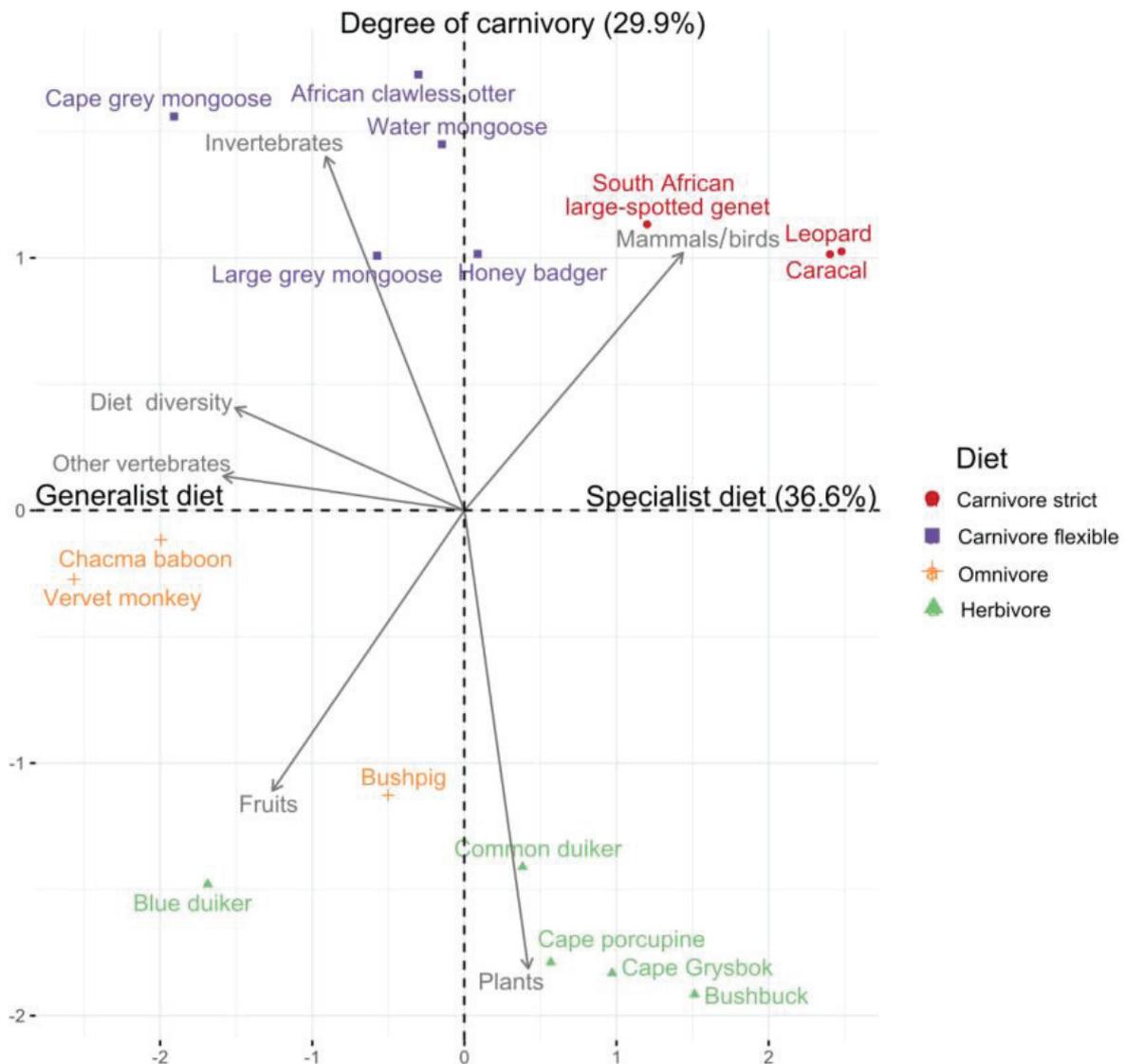
Zimmermann, A., McQuinn, B., & Macdonald, D. W. (2020). Levels of conflict over wildlife: Understanding and addressing the right problem. *Conservation Science and Practice*, 2(10). <https://doi.org/10.1111/csp2.259>

**Supplementary material for manuscript 5** Combining local ecological knowledge with camera traps to assess the link between African mammal life history traits and their use of anthropogenic landscapes

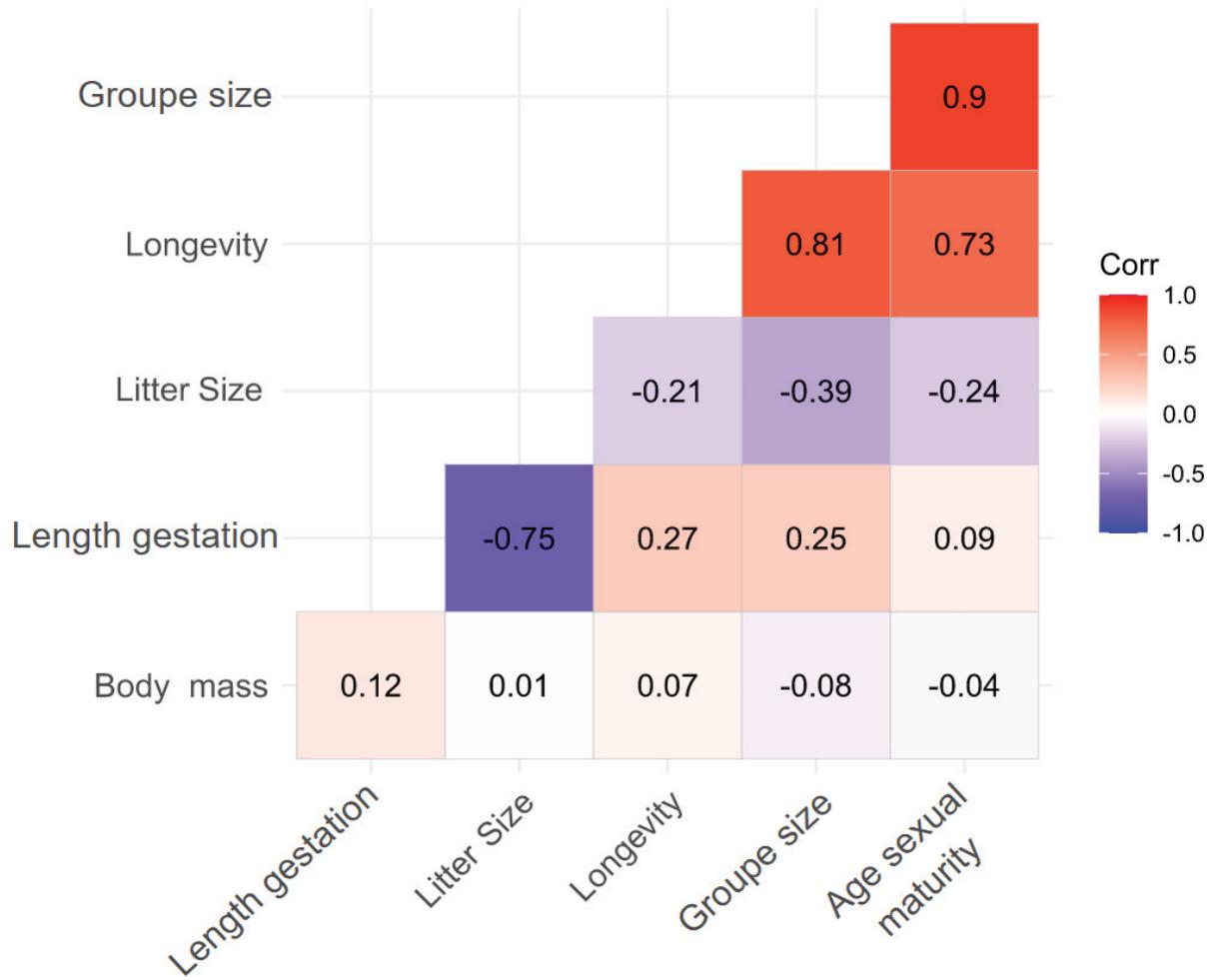
**Figures**



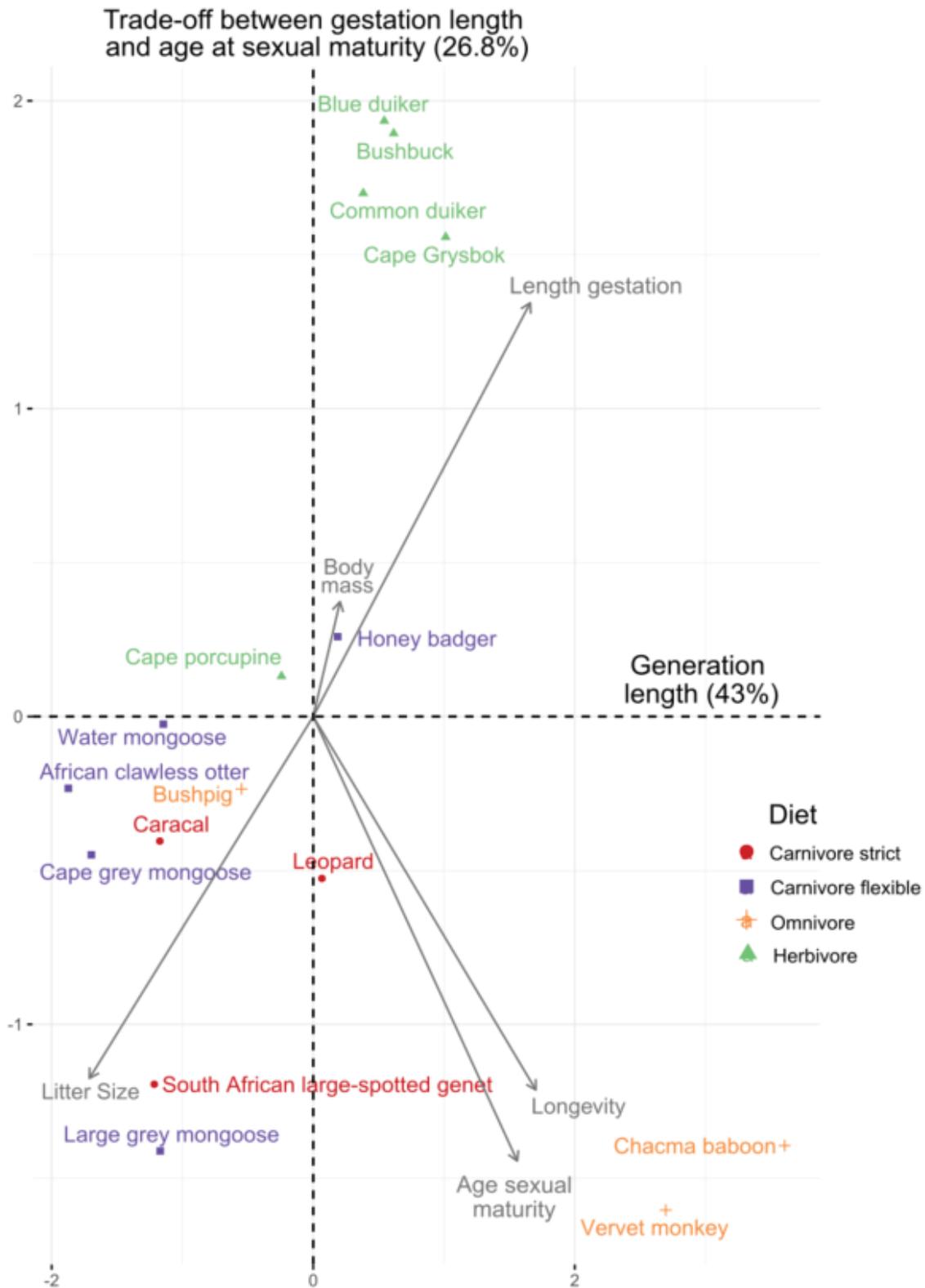
**FIGURE S1** Correlation between the variables used in the Principal Component Analysis on the diet of species.



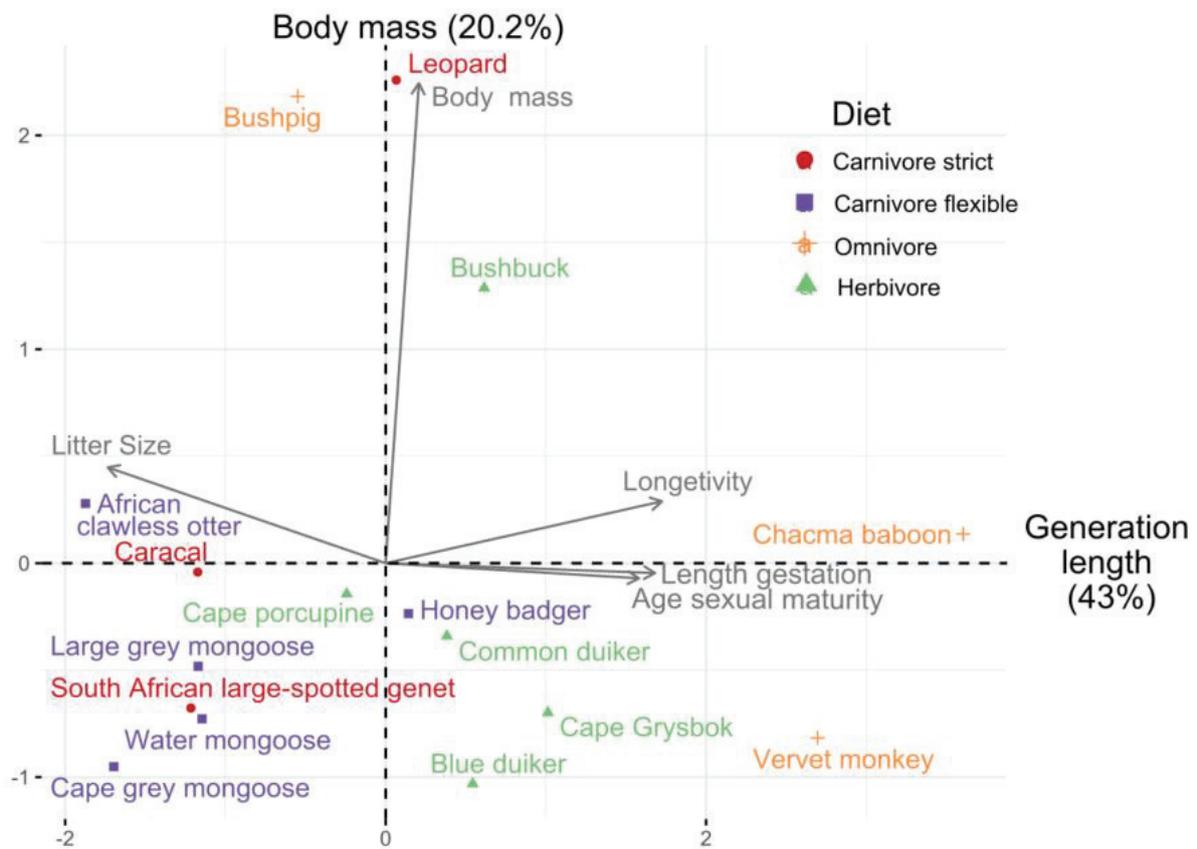
**FIGURE S2** Results of the first two axis of the Principal Components Analysis on mammal species diet: the first axis to describe a gradient from a generalist (left) to a specialist (right) diet and the second axis a gradient of carnivory, with carnivores and top and herbivores at the bottom. For the analyses, we took the inverse of the first axis, so that a positive value represents species with a generalist diet.



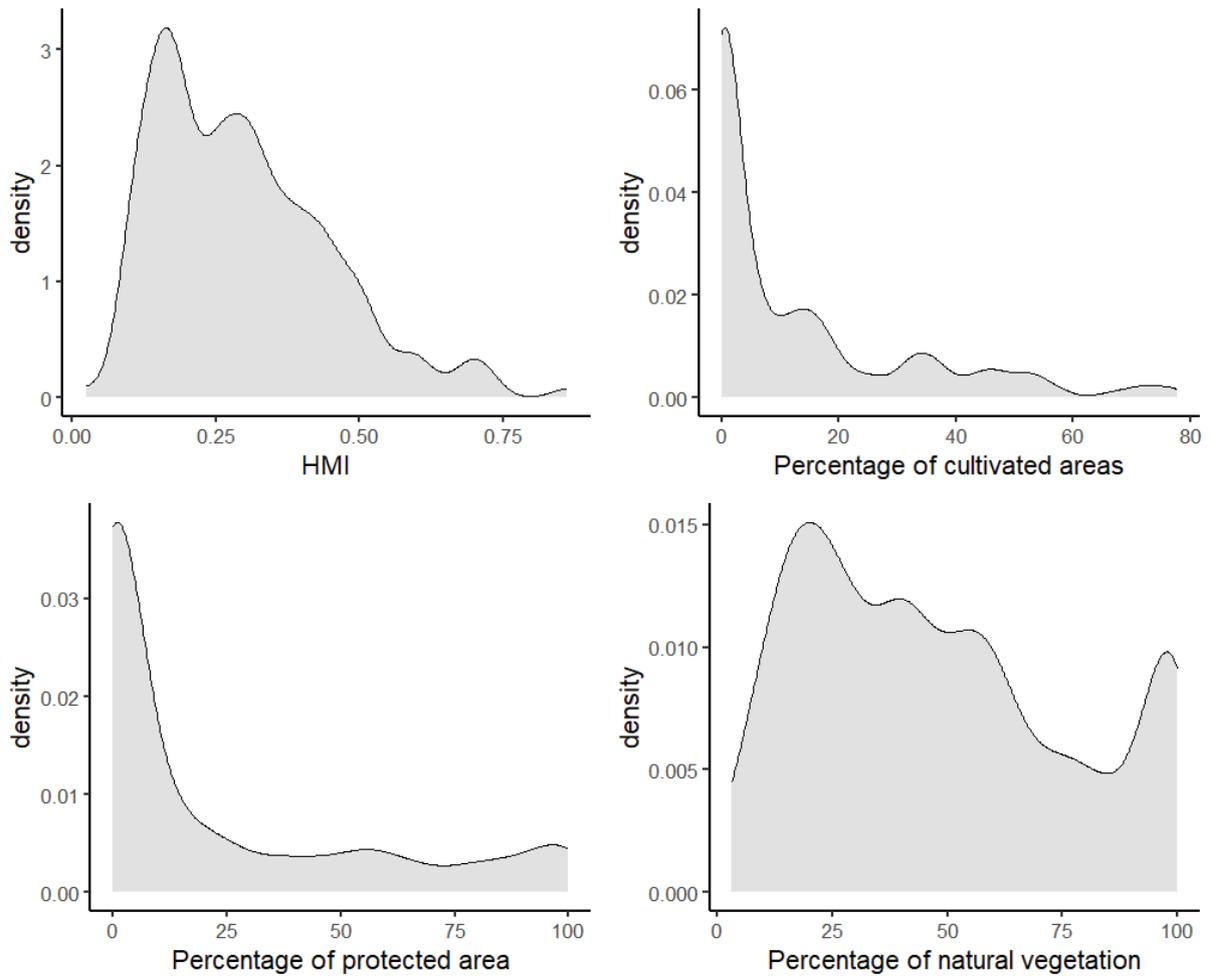
**FIGURE S3** Correlation between the variables used in the Principal Component Analysis on the r/K strategy.



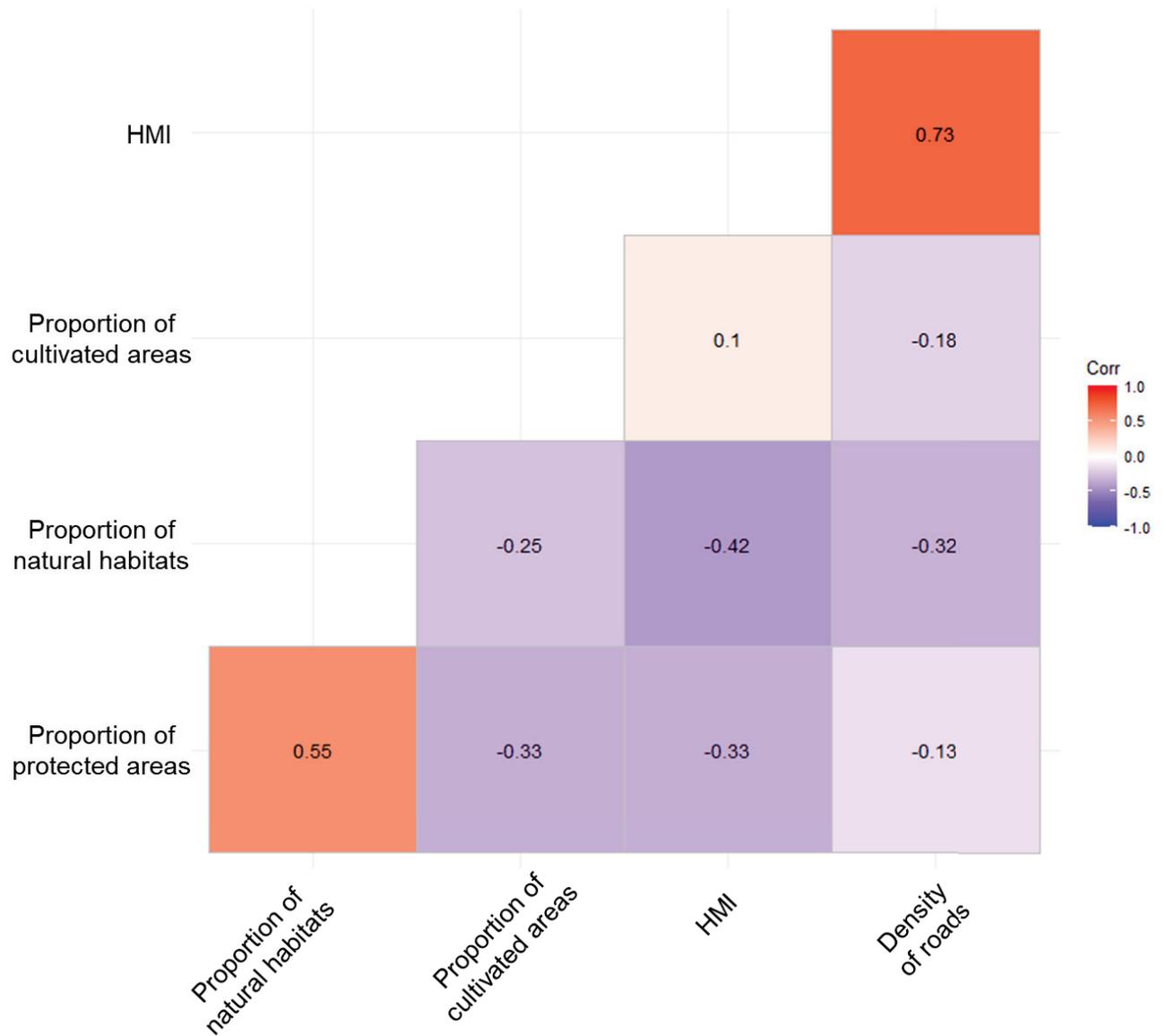
**FIGURE S4** Results of the first two axis of the Principal Components Analysis on mammal species r/K strategy: the first axis represents a gradient from species with a short (left) to long (right) generation length, the second axis express a trade-off between gestation length and age at sexual maturity



**FIGURE S5** Results of the first and third axis of the Principal Components Analysis of mammal species  $r/K$  strategy of the Garden Route. The third axis represents the body mass of the species.



**FIGURE S6** Distribution of the four variables used in the generalized linear model.



**FIGURE S7** Correlation between the candidate variables used in the generalized linear model. We only used variables with a correlation under 0.7: the proportion of cultivated areas, the proportion of natural habitats, the proportion of protected areas and the Human Modification Index (HMI).

## Tables

**TABLE S1** Description of the proportion of type of resources diet as well as various variables describing the traits of each species, extracted from EltonTraits and PanTHERIA database (Jones et al. 2009; Wilman et al. 2014).

English name	Order	Invertebrates	Mammals/ birds	Other vertebrates	Fruit	Plants	Diversity of diet	Body mass (g)	Gestation length (d)	Home range (km <sup>2</sup> )	Average litter Size	Longevity (m)	Solitary or social	Sexual Maturity age (d)
<b>African clawless otter</b>	Carnivora	80	0	0	0	0	0.5	18999.8	63	99.7	2.6	132	Social	371.23
<b>Blue duiker</b>	Artiodactyla	0	0	10	70	20	0.8	4896.1	205	0.006	1	144	Solitary	351.59
<b>Bushbuck</b>	Artiodactyla	0	0	0	0	100	0	43250.4	182.5	0.02	1	156	Solitary	431.61
<b>Bushpig</b>	Artiodactyla	0	10	0	40	40	1.2	48781.3	121.7	4.5	2.7	240	Family	585
<b>Cape grey mongoose</b>	Carnivora	70	0	20	0	10	0.8	797	50	3.8	2.3	104.5	Solitary	591.83
<b>Cape grysbok</b>	Artiodactyla	0	0	0	10	90	0.3	10249.9	210	0.4	1	168	Solitary	630
<b>Cape porcupine</b>	Rodentia	0	0	0	20	80	0.5	14936.0	93.5	1.3	1.5	240	Family	438.45
<b>Caracal</b>	Carnivora	0	100	0	0	0	0	13749.9	71.5	293.9	2.3	204	Solitary	437.27
<b>Chacma baboon</b>	Primates	20	0	10	40	10	1.5	17729.4	185.9	9.1	1	540	Social	1543.35
<b>Common duiker</b>	Artiodactyla	0	10	0	20	70	0.8	15639.2	174.9	1	1	172	Solitary	293.14
<b>Honey badger</b>	Carnivora	20	40	0	0	10	1.5	8500	181.5	350	2.4	318	Solitary	270
<b>Large grey mongoose</b>	Carnivora	30	20	0	10	0	1.5	2980.0	75.9	2.2	3	240	Solitary	729.99
<b>Leopard</b>	Carnivora	0	100	0	0	0	0	52038.2	96.7	123	2.1	276	Solitary	810.68
<b>South African large-spotted genet</b>	Carnivora	10	70	0	0	0	0.8	2066.6	71.5	0.04	2.8	180	Solitary	841.82
<b>Vervet monkey</b>	Primates	20	0	20	40	20	1.3	4993	140	1.7	1	384	Social	1825
<b>Water mongoose</b>	Carnivora	40	30	0	0	0	1.3	3300	77.3	1.7	2	209	Solitary	234.83

**TABLE S2** Proportion of variance explained by each axis and cumulative variance explained for the Principal Components Analysis of mammal species diet.

	<b>Inertia</b>	<b>Cumulative inertia (%)</b>
<b>Axis 1</b>	2.198387	36.64
<b>Axis 2</b>	1.794319	66.55
<b>Axis 3</b>	1.038488	83.85
<b>Axis 4</b>	0.697454	95.48
<b>Axis 5</b>	0.266386	99.92
<b>Axis 6</b>	0.004966	100.00

**TABLE S3** Results of the Principal Components Analysis of mammal species diet. Factor loadings for each trait on each axis are shown for the fourth first axis.

	<b>Axis 1</b>	<b>Axis 2</b>	<b>Axis 3</b>	<b>Axis 4</b>
<b>Invertebrates</b>	-0.4390459	0.67597152	0.56272109	-0.007758839
<b>Mammals/birds</b>	0.6929827	0.49216136	-0.49125733	-0.159590500
<b>Other vertebrates</b>	-0.7649179	0.06554119	-0.01715515	-0.590612015
<b>Fruit</b>	-0.6085880	-0.53543550	-0.49935837	-0.089430664
<b>Plants</b>	0.2027380	-0.87505511	0.40459442	0.040198771
<b>Diet diversity</b>	-0.7271994	0.19608899	-0.25913220	0.559900038

**TABLE S4** Proportion of variance explained by each axis and cumulative variance explained for the Principal Components Analysis of mammal species r/K strategy.

	<b>Inertia</b>	<b>Cumulative inertia (%)</b>
<b>Axis 1</b>	2.1509	43.02
<b>Axis 2</b>	1.3386	69.79
<b>Axis 3</b>	1.0094	89.98
<b>Axis 4</b>	0.3447	96.87
<b>Axis 5</b>	0.1564	100.00

**TABLE S5** Results of the Principal Components Analysis of mammal species r/K strategy. Factor loadings for each trait on each axis are shown for the fourth first axis.

	<b>Axis 1</b>	<b>Axis 2</b>	<b>Axis 3</b>	<b>Axis 4</b>
<b>Body mass</b>	0.09046633	0.1644300	0.97685585	0.1024762
<b>Length of gestation</b>	0.73191881	0.5926121	-0.02000858	-0.2580028
<b>Litter size</b>	-0.75479068	-0.5183730	0.19486009	-0.2899434
<b>Longevity</b>	0.75076559	-0.5349466	0.12592212	-0.3167620
<b>Age of sexual maturity</b>	0.68821678	-0.6368094	-0.03078583	0.2884758

**TABLE S6** Estimates, standard error and p-value for the generalized linear regression models testing the effect of anthropogenic variables on species responses.

<b>Species</b>	<b>Anthropogenic variables</b>	<b>Estimate</b>	<b>Standard error</b>	<b>p-value</b>
<b>Baboon</b>	Proportion of cultivated areas	0.522	0.203	0.010
	HMI	-0.364	0.191	0.057
	Proportion of natural habitats	0.484	0.236	0.040
	Proportion of protected area	-0.624	0.240	0.009
<b>Blue duiker</b>	Proportion of cultivated areas	0.643	0.415	0.122
	HMI	0.466	0.379	0.219
	Proportion of natural habitats	1.537	0.494	0.002
	Proportion of protected area	0.378	0.318	0.235
<b>Bushbuck</b>	Proportion of cultivated areas	0.196	0.196	0.315
	HMI	-0.411	0.196	0.036
	Proportion of natural habitats	0.612	0.270	0.023
	Proportion of protected area	0.046	0.274	0.868
<b>Bushpig</b>	Proportion of cultivated areas	0.219	0.192	0.254
	HMI	-0.939	0.225	0.000
	Proportion of natural habitats	0.470	0.246	0.056
	Proportion of protected area	-0.055	0.247	0.823
<b>Cape grysbok</b>	Proportion of cultivated areas	0.386	0.225	0.086

	HMI	-0.241	0.271	0.375
	Proportion of natural habitats	0.189	0.307	0.537
	Proportion of protected area	-0.488	0.321	0.128
	Proportion of cultivated areas	0.588	0.189	0.002
<b>Caracal</b>	HMI	-0.648	0.223	0.004
	Proportion of natural habitats	-0.315	0.227	0.165
	Proportion of protected area	0.043	0.223	0.848
	Proportion of cultivated areas	-0.193	0.282	0.495
<b>Common duiker</b>	HMI	-0.651	0.299	0.030
	Proportion of natural habitats	-0.807	0.406	0.047
	Proportion of protected area	0.131	0.353	0.712
	Proportion of cultivated areas	0.476	0.198	0.016
<b>Honey badger</b>	HMI	-0.813	0.255	0.001
	Proportion of natural habitats	0.187	0.235	0.427
	Proportion of protected area	-0.213	0.227	0.348
	Proportion of cultivated areas	0.575	0.193	0.003
<b>Large-spotted genet</b>	HMI	-0.688	0.215	0.001
	Proportion of natural habitats	0.306	0.222	0.168
	Proportion of protected area	0.247	0.222	0.266
	Proportion of cultivated areas	0.101	0.256	0.693
<b>Leopard</b>	HMI	-1.111	0.365	0.002
	Proportion of natural habitats	0.191	0.274	0.485
	Proportion of protected area	-0.283	0.263	0.282
	Proportion of cultivated areas	-0.123	0.311	0.694
<b>Otter</b>	HMI	-0.747	0.390	0.056
	Proportion of natural habitats	-0.053	0.349	0.879
	Proportion of protected area	-0.666	0.403	0.098
	Proportion of cultivated areas	0.581	0.187	0.002
<b>Porcupine</b>	HMI	-0.138	0.179	0.441
	Proportion of natural habitats	-0.196	0.210	0.351
	Proportion of protected area	0.095	0.208	0.648
	Proportion of cultivated areas	0.646	0.206	0.002
<b>Vervet monkey</b>	HMI	-0.098	0.182	0.590
	Proportion of natural habitats	0.191	0.216	0.376
	Proportion of protected area	-0.252	0.215	0.241

**TABLE S7** Estimates, standard error and p-value for the linear regression models testing the effects of species trait values (first two principal components from the trait PCA, see Table S3) on species responses from the estimates of the general linear model

<b>Anthropogenic variables</b>	<b>Traits</b>	<b>Estimate</b>	<b>Standard error</b>	<b>p-value</b>
<b>Proportion of cultivated area</b>	Generalist diet	0.046	0.053	0.397
	Body mass	-0.126	0.071	0.103
	Generation length	0.059	0.055	0.299
	Degree of carnivory	-0.010	0.064	0.874
	Trade-off between gestation length and age at sexual maturity	-0.071	0.066	0.304
<b>Human Modification Index</b>	Generalist diet	0.139	0.067	0.064
	Body mass	-0.254	0.088	0.015
	Generation length	0.118	0.076	0.148
	Degree of carnivory	-0.175	0.078	0.045
	Trade-off between gestation length and age at sexual maturity	0.109	0.095	0.277
<b>Proportion of protected area</b>	Generalist diet	-0.039	0.061	0.534
	Body mass	-0.051	0.090	0.582
	Generation length	-0.064	0.062	0.324
	Degree of carnivory	-0.080	0.069	0.274
	Trade-off between gestation length and age at sexual maturity	0.093	0.074	0.234
<b>Proportion of natural habitats</b>	Generalist diet	0.133	0.096	0.193
	Body mass	0.002	0.153	0.992
	Generation length	0.088	0.106	0.426
	Degree of carnivory	-0.080	0.120	0.517
	Trade-off between gestation length and age at sexual maturity	0.066	0.130	0.621





## General discussion



*« Human identity is no longer defined by what one does, but by what one owns. But we've discovered that owning things and consuming things does not satisfy our longing for meaning. We've learned that piling up material goods cannot fill the emptiness of lives which have no confidence or purpose. »*

*Jimmy Carter  
Malaise Speech, 1979*



## 1 | Summary of the main results

Ecosystems and associated communities are complex and cannot be simplified to be easily understood (Montgomery et al. 2019). This calls for attempts to simultaneously tackle as many species as possible to better describe the diversity of responses and the emerging complexity of entangled processes. This *PhD* thesis aimed at documenting the spatio-temporal use of multifunctional anthropogenic landscapes by African mammals, by studying the mammal community (species over 500 g only) in the multifunctional landscapes of the GRBR using CTs and LEK. The goal was to understand what allows large mammal species to persist in landscape mosaics shaped by human activities by testing hypotheses that may influence their occurrence along protection and human disturbance gradients.

### 1.1 | Monitoring mammals in anthropogenic landscapes

First, our research work tested methods to monitor mammals in anthropogenic landscapes. The first manuscript showed that the best height to set up CTs to study human-wildlife interactions in the GRBR was 50 cm, in agreement with other studies monitoring mammal communities (Pardo et al. 2021), which we subsequently used for the CTs survey. We used CTs to document spatio-temporal activity of species (O'Connell et al. 2011), in the second manuscript. However, other factors can affect the detection of species such as animal behavior and ecology, CT itself or the set-up and design, which must be taken into account (Hofmeester et al. 2019; Kays et al. 2020). An alternative method, that can be particularly interesting to implement in anthropogenic landscapes is LEK, which we tested in the third manuscript. LEK provided valuable information on fine-scale descriptions of the landscapes, such as resident's practices and habitats, as well as perceptions about wildlife, with little time and low cost (Bonney et al. 2009; Bennett et al. 2017; Zwerts et al. 2021). However, this method sometimes led to misidentifications and for example, in our case, it was not possible to distinguish the different species of mongooses, whereas it was with the CTs. The comparison of CTs and LEK showed that both methods effectively detected large species, whereas smaller species and especially mesocarnivores such as mongooses were difficult to identify by humans (manuscript 4). This highlights the importance of assessing the level of knowledge of respondents to obtain reliable data (Brittain et al. 2022). The survey detected rare species such as otters or leopards more often, suggesting that in an anthropogenic context, people can be good sentinels for monitoring mammals, whereas CTs are interesting for areas where humans do not go, such as the dense forest of the GRNP that can be difficult to monitor daily. Furthermore, we got very contrasted results with our analysis with the survey data and low spatial effect from the occupancy modeling based on the CTs data. One reason could be the large scale chosen for the CTs grid, which does not capture fine scale responses in mosaic landscapes such as the GRBR. These fine scale responses were better documented using

observation at the properties level in manuscript 3. Combining the two methods enabled us to increase the study area coverage and the number of detections. CTs data confirmed the presence mentioned by respondents of the survey, and LEK confirmed the absence detected by CTs, giving some form of robustness to the data. Combining the methods requires well-designed and compatible protocols, but is a promising way to cover heterogeneous landscapes with diverse land use and human presence. Both methods allowed us to engage with various stakeholders, promoting discussions about wildlife and conservation, as well as land use planning.

## 1.2 | Testing the most appropriate variables to study anthropodependence

Manuscripts 2 and 3 documented the use of anthropogenic landscapes by mammals, testing the conceptual framework of anthropodependence developed by Hulme-Beaman et al. (2016). The manuscript 2 demonstrated the diverse responses of mammals to inhabit human-modified habitats, mostly to human disturbance variables (density of roads and distance to infrastructures). Adding variables of human disturbance, as suggested by other authors (Nickel et al. 2020; Suraci et al. 2021) to the Hulme-Beaman et al. (2016) framework is valuable to describe species sensitivity. The main temporal niche (diurnal, nocturnal or crepuscular) was not the principal explanation for species presence in anthropogenic landscapes, but we recorded a reduction of mammal temporal niche overlap with humans in areas with higher probability of human encounters suggesting that direct temporal avoidance facilitated mammal use of human-dominated habitat (Gaynor et al. 2018; Van Scoyoc et al. 2023). We recommend considering the temporal overlap with humans to complement the Hulme-Beaman et al. (2016) framework as it can explain the strategy developed by species to use anthropogenic landscapes. The manuscript 3 used LEK which provided a more precise description of property attributes such as availability and type of anthropogenic resources, which were lacking in our first approach (manuscript 2) to inform upon the dietary overlap axis developed in the Hulme-Beaman et al. (2016) framework. As previously, we added human disturbance variables (structural disturbances and interferences), as well as variables on availability of anthropogenic resources and natural habitats. It confirmed that species exhibited unique responses but were globally negatively impacted by structural disturbances. Considering human disturbances alongside resource availability and habitat attributes provided a more accurate description of species tolerance of or sensitivity to human activity. Hulme-Beaman et al. (2016) framework is a relevant way to classify mammals in anthropogenic contexts, but including human disturbances and temporal activity gives a more complete description of mammal use of anthropogenic environments. It adds a dimension of tolerance and behavioral adjustment that improves our understanding of how these species are able to use anthropogenic matrices.

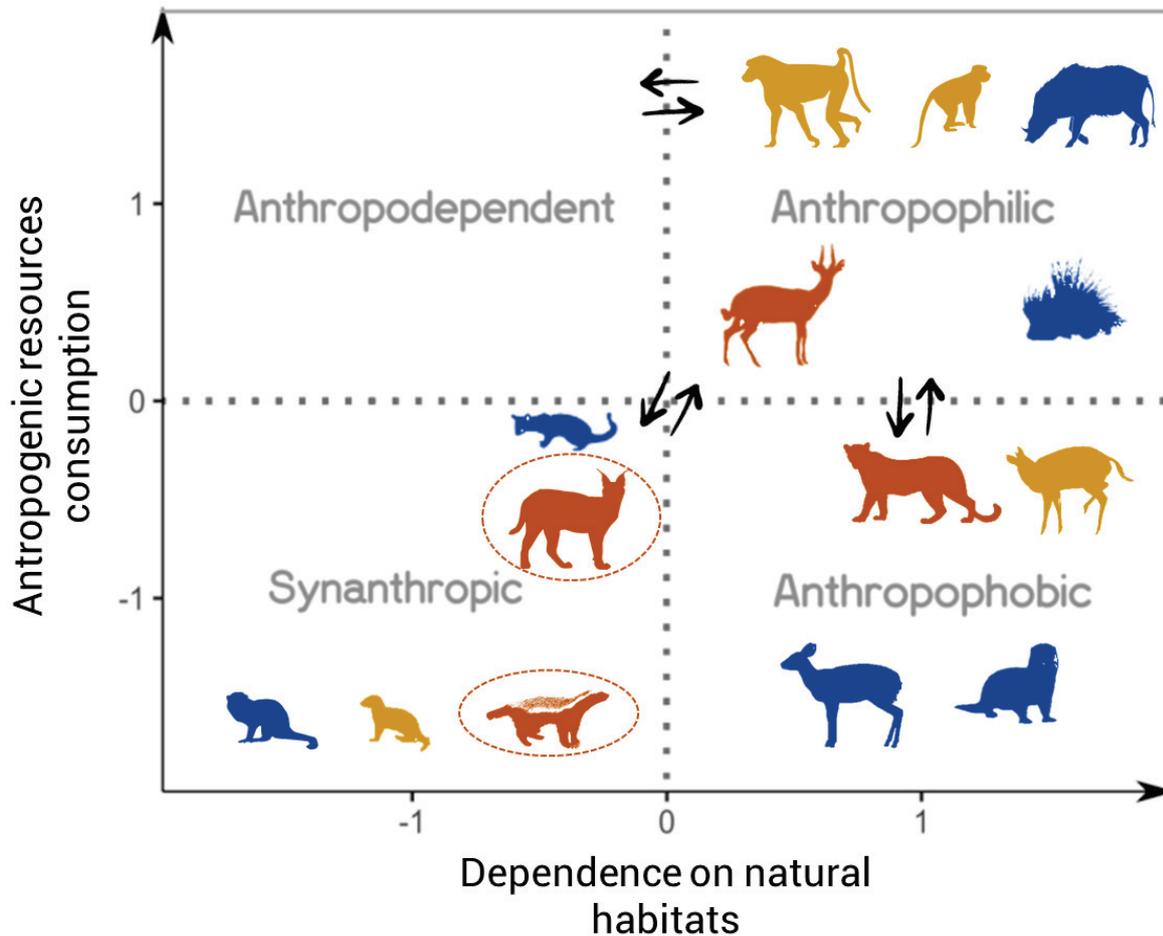
### 1.3 | Species classification using the anthropodependence framework

Manuscripts 2, 3 and 5 described the ecological responses of mammals in anthropogenic landscapes. Our results suggested that the species occurring in the GRBR were relatively well adapted to humans and their activities, and adopted different strategies to adapt to this multifunctional environment. Finally, manuscript 5 showed the selection of some life-history traits in anthropogenic landscapes, which may lead to a homogenization of the community towards generalist species and not strict carnivores. Furthermore, highly modified areas were more favorable to smaller species. These results confirmed that some traits facilitated the adaptation to human-modified habitats and highlight species towards which conservation efforts should focus to avoid homogenization of mammal community (Newbold et al. 2018; Santini et al. 2019; Suraci et al. 2021). Unfortunately the traits analyses did not include the mongooses, but they have small body mass and generalist diet, which in accordance to manuscripts 2 and 3 suggest their abilities to use anthropogenic areas. Combining results from manuscripts 2 and 3, we summarized the potential classification of the species of the GRBR following the Hulme-Beaman et al. (2016) framework (Figure 14). The bushbuck (*Tragelaphus scriptus*) was the most common species according to both methods, detected on 95% of the CTs and 80% of the properties surveyed, suggesting that it is well adapted to the landscapes of the GRBR. It may benefit from consuming anthropogenic vegetation as suggested by other studies, using humans as a shield, or both (Berger 2007; Jansen van Vuuren et al. 2022). The bushbuck could therefore be considered as an anthropophilic species, although its presence on almost all sites may reflect a synanthropic behavior. Baboons (*Papio ursinus*), vervet monkeys (*Chlorocebus pygerythrus*), porcupines (*Hystrix africaeaustralis*) and bushpigs (*Potamochoerus larvatus*) were also quite present in the areas. They seemed to consume human resources, so they could be considered as anthropophilic. The baboon and the vervet monkey are two diurnal species, tolerant to humans, which probably adapt because of high diet flexibility and great cognition capacities such as learning (Barrett et al. 2019). The porcupine and the bushpig seem more sensitive to humans, but their nocturnal behavior helps them use human-dominated environments by avoiding human encounters. The caracal (*Caracal caracal*), honey badger (*Mellivora capensis*), large-spotted genet (*Genetta tigrina*), Cape grey (*Galerella pulverulenta*) and water mongoose (*Atilax paludinosus*) were relatively common in the GRBR as well, but contrary to the previous species did not seem to depend on human resources, suggesting they could be considered as synanthropic species. They are crepuscular (caracal and honey badger) or nocturnal (water mongoose and large-spotted genet), thus reducing their probability of encountering humans. The exception is the Cape grey mongoose which is diurnal, but whose small size and ability to hide may be enough to persist among humans. The classification can be discussed further for the caracal that has been documented to adapt its diet in urban environments and could therefore also be considered as anthropophilic (Leighton et al. 2022b). Similarly, the large-spotted genet

seems to be opportunist and generalist in its diet which may allow it to consume anthropogenic resources (Roberts et al. 2007; Widdows & Downs 2015, 2017). The blue duiker and the leopard were dependent on natural habitats, not consuming human resources, which would tend to classify them as anthropophobic. However, other studies highlighted the high capacity of leopards to use human-dominated habitats and their capacity to adapt their diet (Brackowski et al. 2012b; Athreya et al. 2013). The low detection of the leopard could then be explained by its solitary behavior and large home range (Swanepoel et al. 2016) or a lower adaptation to human-modified habitats of this GRBR leopard population (Hulme-Beaman et al. 2016). The Cape grysbok, large grey mongoose and otter were detected only on very few occasions, raising questions on their capacities to persist in the GRBR. For otters the design of the study may not have been ideal, as it did not focus on riverine habitats and dams. We do not know if these species always occurred at low density or if this is the results of another phenomenon. Previous studies suggested that otters were not common in the Knysna Forest (Hanekom & Randall 2015). As otters may suffer from persecution by fishermen, pollution from intensive agriculture as well as road kill (Jacques et al. 2014; Ergete et al. 2018), their low density is likely to reflect inadequate ecological conditions as much an aversion for humans. The low detection of these species suggest that they are not performing so well in multifunctional landscapes and they may be anthropophobic, such as the blue duiker and the leopard. A study showed that the Cape grysbok has a selective diet, which might explain its low occurrence in areas characterized by a reduction of its prime habitat, e.g. fynbos and thicket (Child et al. 2016; Jansen van Vuuren et al. 2022). The common duiker raises questions because few people detected it and it was not detected by our CTs grid, but it has been detected on CTs belonging to the Great Brak River conservancy close to the city of Mossel Bay, for reasons we cannot explain. The common duiker usually adapts to anthropogenic landscapes but does not occur in forest, which may explain its few detections (Child et al. 2016). Conservation efforts should focus on these last six species in order to better know their ecology in the GRBR to design proper conservation measures.

To summarize, synanthropic species would rather be small and therefore inconspicuous to live near humans, whereas anthropophilic ones would be larger. This seems to be consistent with the fact that the larger species are less likely to be found in the areas strongly suggested in manuscript 5 and that they like natural areas. Anthropophilic species would be mobile to use anthropogenic areas to steal anthropogenic resources and return to hide in natural areas. Synanthropic species seem to be carnivores with a flexible diet, while anthropophilic species are herbivores or omnivores (Figure 14). Further investigation is required to provide a clear description of traits that may be related to Hulme-Beaman et al. (2016) classification. Furthermore, it should be noted that the community of species on which we have worked represents a truncated community compared with a set of species historically present in the

GRBR, *i.e.* that the species really vulnerable to humans are probably already extinct in the area (Baard et al. 2015). We can, for example, mention the case of the Knysna elephant (*Loxodonta africana*) whose population is now practically extinct (Moolman et al. 2019), while lions (*Panthera leo*), hippopotamus (*Hippopotamus amphibius*) and buffalos (*Syncerus caffer*) no longer exist (Baard et al. 2015). Including information on mammals historically present in the areas could further emphasize the effect of life-history traits, such as the body mass, on species occurrence in human-dominated areas.



**FIGURE 14:** Summary of the responses of mammals of the Garden Route Biosphere Reserve to anthropogenic landscapes translated by their consumption of anthropogenic resources and dependence on natural habitats, adapted from Hulme-Beaman et al. (2016). The species colored in blue are nocturnal, in orange are crepuscular and in yellow are diurnal. The dashed circle represents species that do not adapt their temporal activity in areas with more human activity, while others do. The arrows indicate the additional category where some of the species could be positioned

## 1.4 | Conservation recommendations

My *PhD* thesis results are encouraging overall as they suggest that some species may benefit from a shared Earth (Obura et al. 2021). However, anthropophobic species as well as large body mass species rely on natural places, quiet from human disturbances, such as protected areas, to persist. These species are major conservation issues and show the critical role of protected areas in their protection. The preservation of natural patches of vegetation in anthropogenic matrices, undisturbed, which animals can use, such as CBAs is crucial to allow movements between the different protected areas (Brennan et al. 2022), especially for the GRNP, which is fragmented in several sections. We focused on the effect of protection status but did not investigate in-depth the effect of intactness of the habitat, which is a major issue in the GRBR (Baard & Kraaij 2019). Zungu et al. (2020a) revealed the importance of diverse species of intact undergrowth vegetation and the integrity of the forest habitat. Creating of natural corridors, connected patches of natural vegetation and protected areas will benefit all species, such as synanthropic, which will have more areas to move across the landscapes. However, the proximity between natural and modified habitats will increase interfaces and could create more risks of conflicts with anthropophilic species, which are attracted by human food resources and hide in protected or natural areas (Guerbois et al. 2012). Adequate conservation measures must be developed to reduce these risks as they can undermine sustainable coexistence (Carter & Linnell 2023).

## 2 | Complement our understanding of mammals in anthropogenic landscapes and of the anthropodependence principle

This *PhD* thesis was a first step towards assessing the interactions between wild mammals and humans and their activities. My approach focused on the ecology of mammals, but it was also a way to engage discussions with local stakeholders and create contact between them, SANParks and researchers. These results are the ground for further investigations, which is the aim of the International Research Laboratory Reconciling Ecological and Human Adaptations for a Biosphere-based Sustainability (IRL REHABS). This laboratory results from a partnership, started in 2019, between the University of Lyon 1 and the National Center for Scientific Research (CNRS) in France and the Nelson Mandela University in South Africa. The IRL REHABS focuses on the functioning of the interface between protected areas and surrounding landscapes, and on the nature's contribution to people and human-wildlife coexistence. As a main recommendation, monitoring the area using CTs should continue as a long-term project, to detect potential modifications in species occurrence. The CTs grid is already set up and only the servicing needs to be regularly done. In the future, sending out another questionnaire should be considered to see if species occurrence and distribution changed in the broader GRBR landscape. I am

proposing further options to complement the work done on the anthropodependence classification.

## 2.1 | Fine scale spatial decisions in anthropogenic matrices

As suggested by Fleming and Bateman (2018), living in anthropogenic landscapes could induce some changes on species behavior and ecology requirements. For example, species tend to have smaller home ranges as a consequence of greater food availability (Fleming & Bateman 2018). Studying individual strategies would complement CTs data and enable to draw more precise conclusions on species habitat use. As explained in the general material and methods section, I was not able to investigate fine scale spatial movement during my *PhD* thesis, but such information would be interesting to collect to describe, for example, modification of home range size or movement distance in anthropogenic landscapes in comparison with protected areas (Tucker et al. 2018; Doherty et al. 2021). The mammal community of the GRBR is diverse and would give valuable information on the impact of anthropogenic perturbations on individual strategies.

## 2. 2 | Fine scale temporal decisions in response to humans

In the manuscript 2, we focused on the daily activity patterns of each species and their overlap with human activities, but species could also have developed fine scale responses by avoiding some species or humans that would be interesting to analyze using the existing CTs data. Time-to-event analyses (Karanth et al. 2017; Murphy et al. 2021) or the reciprocal time interval between the detection of two species (species A to species B and species B to species A) would be interesting to carry out to detect these fine-scale behavior changes and complement the results of manuscript 2 (Niedballa et al. 2019). Gilbert et al. (2022b) analyzed the compression of species spatio-temporal niches in areas with high human disturbance in comparison to areas with low disturbance, resulting in most cases with less time between the detection of two species. This analysis could be done using existing CTs data, as we can expect the same trend in the GRBR with a reduction of natural habitats and greater human use of anthropogenic areas, reducing opportunities for wildlife. Gilbert et al. (2022b) also proposed to build a co-occurrence network based on the average time between detection in low and high human disturbance areas, which could provide more knowledge on mammal communities in anthropogenic contexts.

## 2. 3 | Species interactions and consequences for the community

Studying species interactions with humans is important to understand the persistence of mammals in anthropogenic contexts (Worm & Paine 2016). It is also crucial to document the consequences of humans on trophic interactions (Gilbert et al. 2022b; Van Scoyoc et al. 2023).

Studying all the species of a community is needed to be able to inform modifications of communities and test hypotheses on sustainable and resilient shared land. In this *PhD* thesis, we studied each species of the community independently, but it would be interesting to study predator-prey interactions, such as caracal and blue duiker or leopard and baboon but also competitive interactions, such as baboon and vervet monkey or caracal and leopard. This could also be done with the existing CTs data using multi-species occupancy modelling, species distribution modeling or network co-occurrence analysis (Rota et al. 2016; Louvrier et al. 2021; Gilbert et al. 2022b). However, studying pairs of interacting species does not necessarily provide a comprehensive picture of the system, as other species may have an impact on the relationship (Pessoa 2021). Therefore, it is recommended to study high-order interactions as it enables to document the complexity of ecosystems and cascading effects, which could lead to an unbalanced system (e.g. becoming less resilient) (Levine et al. 2017). Species communities are often unique and dependent on the landscapes (Amir et al. 2022). Comparing mammal communities in the GRBR, in modified versus protected areas would thus provide insight into their level of complexity, heterogeneity and resilience capacities (Sévêque et al. 2020; Pessoa 2021). Indeed, more diverse communities often appear more stable and ‘trophic downgrading’ is the expected trend in anthropogenic landscapes (Sévêque et al. 2020; Amir et al. 2022). Research should document communities’ interconnection and how it contributes to biodiversity persistence to develop ‘wise wilding’, and best guide conservation efforts (Martin et al. 2016).

## 2.4 | Assessing mammal anthropogenic resources consumption

This *PhD* thesis mainly lacks information on the diet of mammals in comparison between anthropogenic and protected areas to describe the anthropodependence (Hulme-Beaman et al. 2016). In the appendix 2 and 3, we saw that survey and CTs data could provide some information on species diet. However, this type of data does not provide direct information on mammals’ diet and is insufficient to draw conclusions. Several methods could be used to document the diet of mammals such as doing macroscopic, isotopic or meta-barcoding analysis on scat samples (Nielsen et al. 2018). Proceeding to such diet analysis would be a relevant protocol to set up in the GRBR to complete our understanding of anthropodependence, and test the framework more thoroughly. It would provide insight into mammal species’ consumption of anthropogenic food resources and indicate the proportion of their diet that this represents, which can inform their dependence on anthropogenic resources (Hulme-Beaman et al. 2016). Furthermore, diet data could inform the predator and prey relationships and the modifications of such interactions (Van Scoyoc et al. 2023).

Elizabeth Kennedy-Overton, working at the IRL REHABS in the same landscape, found differences in the diet of chacma baboon troops using protected and most human-modified areas. She showed that the nitrogen ratios of chacma baboon scats were higher in anthropogenic areas suggesting a higher consumption of protein in these areas, which may have consequences on baboons' health (paper in preparation). This complemented the work done by Mazue et al. (2023) in the same area, showing that chacma baboons were consuming anthropogenic resources, and that removing access to bins forced them to spend more time foraging for natural food. Other works from South Africa have documented diets of other mammals in anthropogenic contexts, demonstrating their capacities to take advantage of the new resources available in these environments, such as leopards (Martins et al. 2011; Braczkowski et al. 2012b; Drouilly et al. 2018), caracals (Braczkowski et al. 2012a; Drouilly et al. 2018; Jansen et al. 2019), bushbucks (Jansen van Vuuren et al. 2022), water mongooses (Do Linh San et al. 2020), or genets (Roberts et al. 2007; Widdows & Downs 2015, 2017). A proper protocol should be implemented in the GRBR to complement the existing information, as various populations may have different behaviors and habits (Hulme-Beaman et al. 2016). Furthermore, it is essential to document consumption of anthropogenic food resources by wildlife as it may impact their health, which could lead to a deterioration of their fitness. The new IRL REHABS project in collaboration with Nelson Mandela University project named '*Evolutionary adaptation of chacma baboons diet to anthropogenic environments*', led by Virginie Rougeron is looking at the genetic aspect of the diet adaptation that enables wild animals to become successful species in peri-urban environments.

## 2. 5 | Human perceptions of wild mammals and values

As humans use anthropogenic landscapes daily for their economic or leisure activities, it is crucial to understand how they feel about wildlife. More data were collected during the online survey, which would have been interesting to analyze, as for example the information about the tolerance, motivation and value of informants living in the GRBR (Arias-Arévalo et al. 2017; Tourangeau et al. 2020; Kansky et al. 2021). Indeed, it may play a role in the presence of certain species, by acting as an additional landscape of fear for species (Palmer et al. 2023). For example, human acceptance of a species, seems to play a role in species distribution (Behr et al. 2017). It also gives a better understanding of the perception and tolerance towards wildlife, valuable to take into account for developing sustainable conservation measures (Arias-Arévalo et al. 2017; Tourangeau et al. 2020; Kansky et al. 2021).

### 3 | Towards a shared Earth with wildlife

This section is more reflective and relies on publications to give my views on the triptych: people, nature and wildlife. To change the declining trajectory of the terrestrial biodiversity curve, the global economic model needs to change to include more conservation efforts, sustainable production and consumption (Leclère et al. 2020). Furthermore, to meet conservation targets, there is a need for a radical change in our system, as economic growth seems to be the major cause of biodiversity decline (Büscher et al. 2017). Our values must shift from the current growth paradigm and recognize the planet's limits to develop new relationships between nature, humans and wildlife. (Martin et al. 2016). Incorporating '*externalities*', which represent the cost or benefit of an action for ecosystems, is not directly considered in general production systems, but are essential to take into account to charge those who destroy the environment and reward those who protect it. The consequences of an action may impact surrounding stakeholders, for instance the use of pesticides, and thus should be integrated (Lovell & Johnston 2009). However, one should remember that nature is not an externality but it is the reason why life exists on Earth (Locke et al. 2021). Preserving biodiversity has to start with reducing overproduction, changing our way of consumption, shifting to a more vegetarian diet and reducing food waste (Leclère et al. 2020).

#### 3.1 | The value of wildlife in the ecosystem

Biodiversity plays a fundamental role in ecosystem functioning (Wilson et al. 2020; Folke et al. 2021). Animals are part of the intertwined natural system and their diversity are essential for maintaining ecosystem services (Ceaşu et al. 2019). They influence these services including vegetation production, pollination and seed dispersal, habitat modification and pathogen transfer to cite a few (Wilson et al. 2020). Frugivorous, such as the blue duiker are essential to disperse seeds of the indigenous forest of the GRBR (Venter et al. 2016a). Likewise, baboons play a major role in plants seeds dispersion (Hoffman et al. 2016b). The caracal is an apex predator, regulating of prey and mesocarnivore populations (Avenant et al. 2016), while smaller carnivores, such as the Cape grey mongoose control the population of prey like rodents (Do Linh San et al. 2016). People use and modify their environment, but modifications of animal behavior impact ecosystem integrity and species interactions, which disrupt ecosystem services on which humans depend (Fischer et al. 2015; Wilson et al. 2020). The protection of animals as well as the protection of their environment is inevitable to maintain ecosystem services and is therefore critical for the future of the Anthropocene (Leclère et al. 2020; Folke et al. 2021). Büscher et al. (2017) proposed considering natural resources and ecosystems as global public goods to reduce their destruction and properly deal with inequalities through conservation (Martin et al. 2016).

### 3.2 | Create natural space to share

The implementation of protected areas is a major tool for conservation, but raises questions on its location, what will happen to the people who live there, who will be in charge of this new protected areas (community or State-managed) and how will the benefits of it be shared locally and globally (Büscher et al. 2017). Furthermore, some protected areas are isolated, which may limit their effectiveness for conservation (Rodrigues & Cazalis 2020; Brennan et al. 2022). Ensuring connectivity between protected areas is therefore critical to maintain links between wild animal populations, which requires restoring and designing spaces where animals can move freely into anthropogenic matrices (Brennan et al. 2022). Sharing the land between people and biodiversity could even lead to solutions accepted by all stakeholders, constituting an effective and equitable method to build coexistence (Obura et al. 2021). As stated by Blanc (2020), believing that nature will be preserved where there are no humans may encourage people to damage even more areas where humans live, which cannot be a sustainable solution for biodiversity conservation. The GRBR is an asset for testing local solutions to the global issue of halting biodiversity loss.

The Collaborating Across the Landscape to Mitigate impacts of development (CALM) framework aims to put nature at the center of land use planning to build more resilient landscapes and have sustainable development in areas where social and ecological values are respected (Fauna & Flora International 2021). The framework has been conceived for multifunctional landscapes and integrated landscape approaches. The CALM framework follows four steps: (1) gathering information on the landscapes (biodiversity and ecosystem) to assess the state of knowledge, (2) identifying future threats on the landscapes; steps 1 and 2 aim at highlighting the priorities for conservation; (3) planning what needs to be done (based on the Mitigation and Conservation Hierarchy framework) and (4) implementing actions, *i.e.* practical application of the measures in the landscapes by all stakeholders (Fauna & Flora International 2021). The framework is seen through a socio-ecological lens (Fauna & Flora International 2021). Socio-ecological systems are a framework to understand interactions between environments and society, since they are interconnected (Fischer et al. 2015). The Mitigation and Conservation Hierarchy framework developed by Milner-Gulland et al. (2021) before the COP15 is a four-step approach to define clear actions for conservation: 1) **refrain** from causing negative impacts, 2) **reduce** the impacts that are caused, 3) **restore** impacted nature and 4) **renew** our relationship with nature.

This *PhD* thesis provided a baseline on the current state of mammals in the GRBR. Population growth and especially urban sprawl seem to be the major threat for mammals. The Mitigation and Conservation Hierarchy framework could be used to provide some guidance for the future of the GRBR (Milner-Gulland et al. 2021). (1) **Refrain**; protect the Critical Biodiversity Areas from urban

development and protect all the remaining natural vegetation. (2) **Reduce**; promote sustainable farming and timber practices. (3) **Restore**; clear alien species and replant indigenous vegetation such as afro temperate forest species or fynbos. Clearing is regularly done by SANParks in the GRNP and every landowner must do it, as it is written in the law. Among other things, as in most places, enforcement is unfortunately not always convincing enough to get everyone on board. (4) **Renew**; leave space on each property for wildlife to flourish, leave a pet-free area to reduce the predation on wildlife (fence a part around the house) or create new natural spaces where clearing has occurred by maintaining the natural vegetation.

To develop a new sustainable socio-ecological system, all stakeholders (researchers, citizens and governments) will have to collaborate (Fischer et al. 2015). Practitioners and local communities should be consulted to define research priorities (Fischer et al. 2015). Conservation planning can prove very useful as it highlights potential conflict areas and adapt to mitigate or even avoid them (Saenz et al. 2013). For these conservation projects to emerge and be sustainable, funding needs to be secured for long-term projects to detect and create change (Fischer et al. 2015).

### 3.3 | Coexistence with wildlife

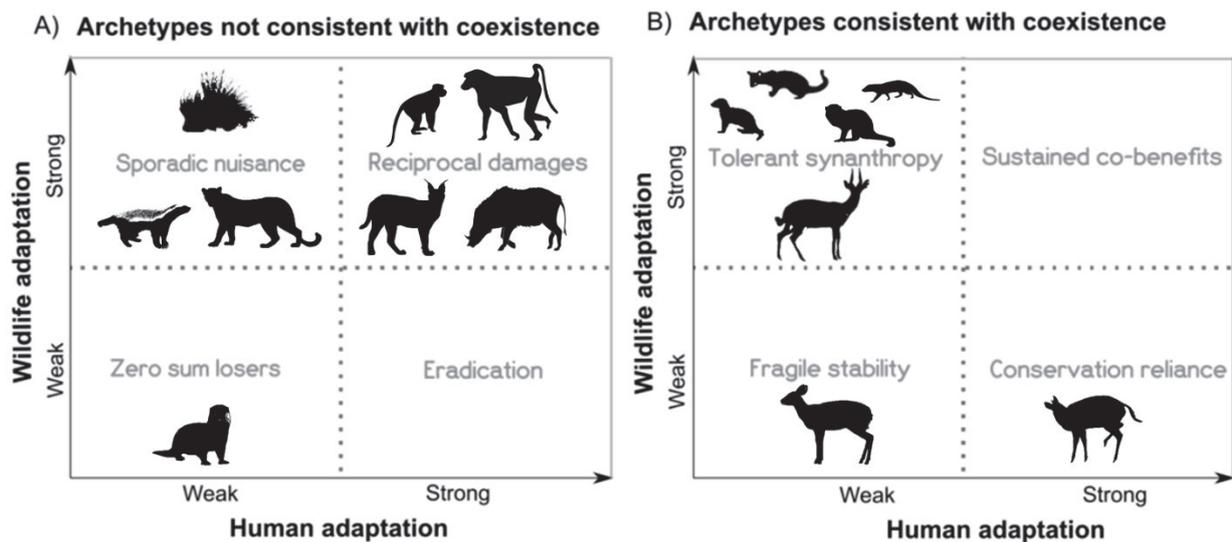
The coexistence between humans and wildlife is not always easy, and coexistence with larger carnivores can be even trickier (Inskip & Zimmermann 2009; McInturff et al. 2021). Coexistence inequality and intolerance are the main threats to coexistence (Jordan et al. 2020). **Inequalities** refer to the fact that, often in conservation, northern countries and urban populations harvest more benefits from conservation, whereas southern countries and rural populations pay higher costs (Jordan et al. 2020). **Tolerance**, which varies according to social and cultural norms and values, is often the limiting point for coexistence (Treves & Bruskotter 2014). The main risks of coexistence with large carnivores for humans are depredation on livestock, competition with hunters and attacks on humans (Carter & Linnell 2016). The fear linked to the presence of carnivores needs to be carefully considered as it raises environmental justice concerns (McInturff et al. 2021). One of the challenges for sustainable coexistence is to promote conservation measures, while including and considering people affected by conflicts with wildlife (Jordan et al. 2020). Win-win scenarios, where conservation goals and human well-being are positively impacted are uncommon and hard choices or trade-offs often need to be made (McShane et al. 2011). Conservationists should be realistic about the impact of conservation measures on people to honestly discuss with them and find appropriate solutions (McShane et al. 2011). Furthermore, to coexist, both humans and wildlife need to adapt their behavior to avoid negative and risky experiences (Carter & Linnell 2023). Several measures can be used to enhance coexistence such

as public awareness campaigns, change of agricultural practices, spatial partitioning or losses compensation (Carter & Linnell 2016), but coexistence will not be possible without human agreement and involvement (Carter & Linnell 2023). Engagement with stakeholders enables one to find bottom-up solutions and be more confident that international recommendations will be successfully applied at the local scale, as stakeholders can become part of the enforcement of the conservation measures (Carter & Linnell 2016), as well as the source of local innovation.

As more and more research advocates that conservation goals cannot be achieved without people (Martin et al. 2016; Folke et al. 2021; McInturff et al. 2021; Carter & Linnell 2023), McInturff et al. (2021), proposed an environmental justice framework to help develop effective conservation programs. They advocate to consider (1) **multispecies justice**, which concerns humans and non-humans, (2) **social justice**, which considers human community inequalities through **participatory** (who participate in the decision making process), **disruptive** (who are affected by the conservation actions) and **recognition** (people's history, knowledge is recognized in the process), and (3) **affective justice**, which includes the perception and effects linked to each societal question (McInturff et al. 2021).

Carter and Linnell (2023) synthesized human and wildlife interactions as a function of the adaptation capacity of both parties, and if the mutual adaptation is consistent with coexistence or not (Figure 15). These archetypes could be applied to provide some insight into the coexistence with the mammal species of the GRBR, which could help design adequate conservation measures. The four archetypes not compatible with coexistence are described in the following lines. **Zero sum losers** correspond to weak adaptation of both human and wildlife which will lead to the decline of wildlife populations if nothing is done. We suspect the Cape clawless otter to be in this situation as its detection was very low in the GRBR. **Sporadic nuisance** corresponds to weak adaptation of humans and strong adaptation of wildlife, which does minor damage but the responses from humans do not put local populations in danger. This categorization could correspond to porcupines, leopards and honey badgers. **Reciprocal damages** correspond to strong adaptation of both human and wildlife, which will negatively impact both parties. This could be the case for baboons, vervet monkeys, bushpigs and caracals, since these species are often shot at or even killed in response to the damage they do on poultry or crops. **Eradication** is a strong adaptation of humans but a weak adaptation of wildlife, which leads to their eradication. This case does not seem to be happening in the GRBR. Archetypes of coexistence are described in the following points. **Fragile stability** corresponds to weak adaptation of both humans and wildlife, where they do not impact each other. It could correspond to the grysbok, which seems to persist with difficulty in the GRBR. **Tolerant synanthropy** corresponds to weak adaptation of humans and strong adaptation of wildlife, where people tolerate the presence of the species. In

the GRBR, it seems to apply for genets, bushbucks, and Cape grey, large grey and water mongooses. **Conservation reliance** corresponds to weak adaptation of wildlife but strong adaptation of humans, where actions are taken to protect the species. This could be the case for the blue duiker, whose preferred habitat on which it depends, the forest, has been protected. **Sustained co-benefits** correspond to strong adaptation of both human and wildlife, which positively impact both parties. It is difficult to know if it is in place in the GRBR. In relation to this classification, our recommendations for the GRBR species would be to (1) monitor the Cape clawless otter to understand its decline, and the common duiker and the grysbok to assess the status of the populations (2) find sustainable solutions to share space with baboons, vervet monkeys, porcupines and bushpigs to allow peaceful coexistence, (3) monitor residents' perception of leopards, honey badgers, caracals, baboons, vervet monkeys and bushpigs to make sure it does not turn into eradication.



**FIGURE 15:** Different archetypes of coexistence between people and wildlife, reproduced and adapted from Carter and Linnell (2023)

### 3.4 | Law as a protection tool

Ecosystems and animals do not have the possibility to fight for their rights. International institutions and national legislations have a role to play in conservation in certain areas, to facilitate the application of conservation measures (Carter & Linnell 2023). The classification proposed by Hulme-Beaman et al. (2016) raises the debate of how to apply animal rights. The categorization shows different degrees of dependence on humans for food and space. The concept of dependence served as a basis for the reflection made by Sue Donaldson and Will Kymlicka in their book *Zoopolis: A Political Theory of Animal Rights* (2011). They proposed to classify species into three categories: citizens, residents and wild. **Citizens** will correspond to all

domestic animals living with humans, such as pets or livestock. They will be bound to humans by a social contract. They work for humans (e.g. milk production, mine or drug detection), and in exchange, humans need to protect and care for them. **Residents** will regroup species sharing human landscapes but living independently (e.g. human commensal species). They will have the right to cohabit, but within mutual limits, which are to be defined. Finally, the wild category regroups wild and autonomous species. They are '**sovereign communities**' and have the right to autonomy and respect for their territory and way of life. Citizens mostly apply to domestic animals. Wild mammals can fit into one of the two remaining categories. Anthropophobic corresponds perfectly to the sovereign category. Synanthropic species are more likely to be residents, since we expect them not to impact humans. Anthropophilic and anthropodependent species will also be residents, but they might cross the limit humans can tolerate. Conflicts are likely to happen with these species when they leave protected or natural areas to raid human resources. Furthermore, a recent study showed that more conflicts are to be expected in the future because of climate change and the destruction of natural habitats (Abrahms et al. 2023). These vigilance points should be considered when designing shared landscapes

### 3.5 | The challenges for wildlife to live with humans

Studying if mammals were able to adapt to live close to humans was a first step. Then people need to liberate and create space to share with wildlife. For coexistence to be possible, people need to be involved and accept the cost of the coexistence. Finally, the question remains regarding the implications for wildlife to live close to humans. This requires multidisciplinary approaches to understand the whole system (Ostrom 2007). Living in modified habitats might impact the fitness of the species (Fleming and Bateman, 2018). Fleming and Bateman (2018), hypothesized that species in anthropogenic areas will have faster growth rates or greater reproductive success. For instance, studies on blue tits (*Cyanistes caeruleus*) showed that urban individuals were more aggressive and had higher breath rate than their rural counterparts, and they suggested that this behavior was associated with lower fitness and that the selection in cities could even be maladaptive (Caizergues et al. 2022). Human-dominated areas can lead to ecological traps, defined as the use of poor quality habitat by a species or which leads to an increased risk of mortality, resulting in its rapid decline (Hale & Swearer 2016). Often, species falling into ecological traps use one cue for the habitat choice but fail to perceive the increased risk of mortality. For example, wild dogs (*Lycaon pictus*) in Zimbabwe moved outside of Hwange National Park, where reproductive success is better but the risk of mortality is much higher for them (van der Meer et al. 2014).

Furthermore, human modifications of the land induce a risk of the emergence of new zoonotic diseases in the future (Locke et al. 2021). The COVID-19 pandemic showed how vulnerable our societies are to these threats (Locke et al. 2021). This was not the first pandemic and will not be the last. The overlap between domestic and wild animals can exacerbate the transmission of diseases. Avian influenza, after infecting poultry farming, is now threatening wild birds (Boulinier 2023). Domestic and feral cats are known to be the host of *Toxoplasma gondii*, and could present a higher risk of transmission of the diseases to wild mesocarnivores such as the Tasmanian devil (*Sarcophilus harrisii*), for whom it is lethal, in Tasmania (Hollings et al. 2013). *Toxoplasma gondii* was highly detected (83% of seropositivity) in the population of urban caracals near Cape Town (Serieys et al. 2019). In France, the seroprevalence of brucellosis in an Alpine ibex (*Capra ibex*) population threatens livestock grazing in the same areas (Marchand et al. 2017). The preventive measure advocated by the government was to shoot Alpine ibex to reduce the risks of transmission (FNE 2022). Preventive measures are often detrimental for wildlife. Agricultural practices such as the exclusion of livestock from protected areas could reduce the transmission of disease, e.g. the foot-and-mouth disease between cattle and the African buffalo (*Syncerus caffer*) in Hwange National Park, Zimbabwe (Miguel et al. 2017). Intense surveillance of disease emergence should be advocated and their transmission must be documented (Boulinier 2023). Integrative and multidisciplinary approaches must be developed to bring together human, animal, and ecosystem health into the One health approach (Aguirre et al. 2019).

Living in or close to urban or farming areas can also expose wildlife to potential pollutants. Foraging in urban edges led caracals to be highly exposed to organochlorines, which might have deleterious effects on their health (Leighton et al. 2022a). The same pesticide was also found in leopard blood (van As et al. 2022). In Uganda, 25% of the monitored population of chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park have been detected facial abnormalities or reproductive issues (Krief et al. 2017). This may be caused by the pesticides used in the agricultural areas, in which chimpanzees are raiding crops (Krief et al. 2017, 2022). Murray et al. (2019) found a negative effect of urbanization on wildlife health worldwide. Urban populations are often exposed to more toxic products and parasites, but they could not determine an impact on the stress levels of species (Murray et al. 2019). Another meta-analysis came to the same conclusion regarding the level of stress induced by urban environments (Iglesias-Carrasco et al. 2020). However, glucocorticoid hormones, used to measure the level of stress, were higher in faeces of chacma baboons foraging in more urban areas near Cape Town (Chowdhury et al. 2020), which may suggest a sensitivity of some species or even populations.

The question of wildlife health in human-modified habitats is critical, to ensure that our modified landscapes do not represent ecological traps. Information is, unfortunately, missing on certain

taxa and geographic areas (Murray et al. 2019). Research mainly focused on North America and Europe, showing the value of conducting projects in Africa (Murray et al. 2019). The stressors associated with urban environments (e.g. noise, artificial light, pollution) are multiple and their impact on wildlife could interact with each other (Isaksson 2015). Research should be planned on several mammal species and investigates multiple health metrics such as the effects of toxicants, parasites, stress and body condition to be able to properly assess mammal health (Murray et al. 2019). It is a necessity to address if and how species can evolve in human-modified habitats (Isaksson 2015). The GRBR is the perfect place for such projects.

## 4 | Concluding remarks

Africa is home to an incredibly rich and diverse wildlife, representing 30% of the remaining wild mammal biomass (6Mt) on the planet (Greenspoon et al. 2023), with a Biodiversity Intactness Index above the global average (76,87% for the world and 80.22% for Africa in 2022) (Hill et al. 2018). African countries are playing a major role in conservation of megafauna (Lindsey et al. 2017a). People in the GRBR seemed aware of the incredible luck they have to live in the vicinity of nature and the necessity to protect it. Because of residents' willingness to participate the research process and the available multifunctional landscape, the GRBR could be the perfect place to co-construct with stakeholders and residents, an example of a successful 'shared Earth' model and of sustainable coexistence with wildlife. I am convinced that western countries have much to learn from examples from the global South to develop ways of coexistence with large mammals, especially carnivores. However, no simple solution exists for preserving biodiversity in a multi-stakeholders and complex world and there is no universal solution (Ostrom 2007). Research should be co-constructed to build fair and honest conservation measures that will benefit people and nature (McShane et al. 2011; Bourgeois et al. 2023), and for that, interdisciplinary development appears inevitable (Ostrom 2007). Simultaneously, results and opinions should be shared to find innovative solutions (Trisos et al. 2021). Nature should be respected and preserving biodiversity put at the center of political priorities (Martin et al. 2016). 'Reconciling ecology' should be the first step of this difficult task to design spaces which can be shared between people and wildlife (Rosenzweig 2003; Obura et al. 2021). As said by Martin et al. (2016) '*a key role of conservation science will then be finding ways to increase opportunities for biodiversity and natural processes in all contexts, from natural to semi natural and human built ecosystems*'.



## References





- Abrahms, B., Carter, N.H., Clark-Wolf, T.J., Gaynor, K.M., Johansson, E., McInturff, A., Nisi, A.C., Rafiq, K. & West, L. (2023). Climate change as a global amplifier of human–wildlife conflict. *Nat. Clim. Chang.*, 1–11.
- Aguirre, A.A., Longcore, T., Barbieri, M., Dabritz, H., Hill, D., Klein, P.N., Lepczyk, C., Lilly, E.L., McLeod, R., Milcarsky, J., Murphy, C.E., Su, C., VanWormer, E., Yolken, R. & Sizemore, G.C. (2019). The One Health Approach to Toxoplasmosis: Epidemiology, Control, and Prevention Strategies. *EcoHealth*, 16, 378–390.
- Amir, Z., Moore, J.H., Negret, P.J. & Luskin, M.S. (2022). Megafauna extinctions produce idiosyncratic Anthropocene assemblages. *Sci. Adv.*, 8, eabq2307.
- Anthony G. Rebelo, Charles Boucher, Nick Helme, Ladislav Mucina, & Michael C. Rutherford. (2006). Fynbos Biome. In: *Plants of the greater Cape floristic region, Strelitzia*. pp. 54–219.
- Appleton, M.R., Courtiol, A., Emerton, L., Slade, J.L., Tilker, A., Warr, L.C., Malvido, M.Á., Barborak, J.R., de Bruin, L., Chapple, R., Daltry, J.C., Hadley, N.P., Jordan, C.A., Rousset, F., Singh, R., Sterling, E.J., Wessling, E.G. & Long, B. (2022). Protected area personnel and ranger numbers are insufficient to deliver global expectations. *Nat Sustain*, 5, 1100–1110.
- Arias-Arévalo, P., Martín-López, B. & Gómez-Baggethun, E. (2017). Exploring intrinsic, instrumental, and relational values for sustainable management of social-ecological systems. *E&S*, 22, art43.
- van As, M., Smit, N.J., Wolmarans, N.J. & Wepener, V. (2022). First record of organochlorine pesticides in blood of wild and captive African leopards, *Panthera pardus pardus* (Linnaeus, 1758). *Frontiers in Environmental Science*, 10.
- Athreya, V., Odden, M., Linnell, J.D.C., Krishnaswamy, J. & Karanth, U. (2013). Big Cats in Our Backyards: Persistence of Large Carnivores in a Human Dominated Landscape in India. *PLOS ONE*, 8, e57872.
- Avenant, N.L., Drouilly, M., Power, R.J., Thorn, M., Martins, Q., Neils, A., du Plessis, J. & Do Linh San, E. (2016). A conservation assessment of *Caracal caracal*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, DaviesMostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Baard, J., Durrheim, G., Hanekom, N., Hayes, J.S., Kraaij, T., Kruger, N., Ngubeni, N., Randall, R.M., Russell, I.A., Seydack, A.H.W., Smith, K., Van der Vyer, L. & Vermeulen, W.J. (2015). *Garden Route National Park - State of knowledge*.
- Baard, J.A. & Kraaij, T. (2019). Use of a rapid roadside survey to detect potentially invasive plant species along the Garden Route, South Africa. *Koedoe*, 61, 1–10.
- Barbar, F., Werenkraut, V., Morales, J.M. & Lambertucci, S.A. (2015). Emerging Ecosystems Change the Spatial Distribution of Top Carnivores Even in Poorly Populated Areas. *PLoS ONE*, 10, e0118851.

- Bar-On, Y.M., Phillips, R. & Milo, R. (2018). The biomass distribution on Earth. *Proc Natl Acad Sci USA*, 115, 6506–6511.
- Barrett, L.P., Stanton, L.A. & Benson-Amram, S. (2019). The cognition of 'nuisance' species. *Animal Behaviour*, 147, 167–177.
- Bateman, P.W. & Fleming, P.A. (2012). Big city life: carnivores in urban environments. *Journal of Zoology*, 287, 1–23.
- Batisse, M. (1982). The Biosphere Reserve: A Tool for Environmental Conservation and Management. *Envir. Conserv.*, 9, 101–111.
- Behr, D.M., Ozgul, A. & Cozzi, G. (2017). Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: a case study of the wolf in Switzerland. *J Appl Ecol*, 54, 1919–1929.
- Bennett, N.J., Roth, R., Klain, S.C., Chan, K., Christie, P., Clark, D.A., Cullman, G., Curran, D., Durbin, T.J., Epstein, G., Greenberg, A., Nelson, M.P., Sandlos, J., Stedman, R., Teel, T.L., Thomas, R., Veríssimo, D. & Wyborn, C. (2017). Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation*, 205, 93–108.
- Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.*, 3, 620–623.
- Blanc, G. (2020). *L'invention du colonialisme vert. Pour en finir avec le mythe de l'Eden Africain*. Editions Flammarion.
- Bonneuil, C. & Frescoz, J.-B. (2016). *The shock of the Anthropocene: the earth, history, and us*. Verso, London ; Brooklyn, NY.
- Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V. & Shirk, J. (2009). Citizen Science: A Developing Tool for Expanding Science Knowledge and Scientific Literacy. *BioScience*, 59, 977–984.
- Boulinier, T. (2023). Avian influenza spread and seabird movements between colonies. *Trends in Ecology & Evolution*, S0169534723000319.
- Bourgeois, R., Guerbois, C., Giva, N., Mugabe, P., Mukamuri, B., Fynn, R., Daré, W., Motsholapheko, M., Nare, L., Delay, E., Ducrot, R., Bucuane, J., Mercandalli, S., Le Page, C. & Caron, A. (2023). Using anticipation to unveil drivers of local livelihoods in Transfrontier Conservation Areas: A call for more environmental justice. *People and Nature*, pan3.10446.
- Braczkowski, A., Watson, L., Coulson, D., Lucas, J., Peiser, B. & Rossi, M. (2012a). The Diet of Caracal, (*Caracal caracal*), in Two Areas of the Southern Cape, South Africa as Determined by Scat Analysis. *South African Journal of Wildlife Research*, 42, 111–116.
- Braczkowski, A., Watson, L., Coulson, D. & Randall, R. (2012b). Diet of leopards in the southern Cape, South Africa. *Afr. J. Ecol.*, n/a-n/a.

- Brennan, A., Naidoo, R., Greenstreet, L., Mehrabi, Z., Ramankutty, N. & Kremen, C. (2022). Functional connectivity of the world's protected areas. *Science*, 376, 1101–1104.
- Brittain, S., Rowcliffe, M.J., Kentachime, F., Tudge, S.J., Kamogne-Tagne, C.T. & Milner-Gulland, E.J. (2022). Comparing interview methods with camera trap data to inform occupancy models of hunted mammals in forest habitats. *Conservat Sci and Prac*.
- Brockie, R.E., Sadleir, R.M.F.S. & Linklater, W.L. (2009). Long-term wildlife road-kill counts in New Zealand. *New Zealand Journal of Zoology*, 36, 123–134.
- Brook, R.K. & McLachlan, S.M. (2008). Trends and prospects for local knowledge in ecological and conservation research and monitoring. *Biodivers Conserv*, 17, 3501–3512.
- Brooks, J., Kays, R. & Hare, B. (2020). Coyotes living near cities are bolder: implications for dog evolution and human-wildlife conflict. *Behav.*, 157, 289–313.
- Burgos, T., Salesa, J., Fedriani, J.M., Escribano-Ávila, G., Jiménez, J., Krofel, M., Cancio, I., Hernández-Hernández, J., Rodríguez-Siles, J. & Virgós, E. (2023). Top-down and bottom-up effects modulate species co-existence in a context of top predator restoration. *Scientific Reports*.
- Büscher, B., Fletcher, R., Brockington, D., Sandbrook, C., Adams, W.M., Campbell, L., Corson, C., Dressler, W., Duffy, R., Gray, N., Holmes, G., Kelly, A., Lunstrum, E., Ramutsindela, M. & Shanker, K. (2017). Half-Earth or Whole Earth? Radical ideas for conservation, and their implications. *Oryx*, 51, 407–410.
- Caizergues, A.E., Grégoire, A., Choquet, R., Perret, S. & Charmantier, A. (2022). Are behaviour and stress-related phenotypes in urban birds adaptive? *Journal of Animal Ecology*, 91, 1627–1641.
- Campbell, B.M., Beare, D.J., Bennett, E.M., Hall-Spencer, J.M., Ingram, J.S.I., Jaramillo, F., Ortiz, R., Ramankutty, N., Sayer, J.A. & Shindell, D. (2017). Agriculture production as a major driver of the Earth system exceeding planetary boundaries. *E&S*, 22, art8.
- CapeNature. (2016). Biosphere Reserve - Garden Route Zonation, shapefile downloaded from [errol@gardenroutebiosphere.org.za](mailto:errol@gardenroutebiosphere.org.za).
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J. & Mace, G.M. (2004). Human Population Density and Extinction Risk in the World's Carnivores. *PLoS Biol*, 2, e197.
- Carricondo-Sanchez, D., Odden, M., Kulkarni, A. & Vanak, A.T. (2019). Scale-dependent strategies for coexistence of mesocarnivores in human-dominated landscapes. *Biotropica*, 51, 781–791.
- Carruthers, J. (2017). *National Park Science: A Century of Research in South Africa*. Cambridge University Press.
- Carter, N.H. & Linnell, J.D.C. (2016). Co-Adaptation Is Key to Coexisting with Large Carnivores. *Trends in Ecology & Evolution*, 31, 575–578.

- Carter, N.H. & Linnell, J.D.C. (2023). Building a resilient coexistence with wildlife in a more crowded world. *PNAS Nexus*, 2, pgad030.
- Cazalis, V., Princé, K., Mihoub, J.-B., Kelly, J., Butchart, S.H.M. & Rodrigues, A.S.L. (2020). Effectiveness of protected areas in conserving tropical forest birds. *bioRxiv*, 2020.01.21.912345.
- Ceaușu, S., Graves, R.A., Killion, A.K., Svenning, J.-C. & Carter, N.H. (2019). Governing trade-offs in ecosystem services and disservices to achieve human–wildlife coexistence. *Conservation Biology*, 33, 543–553.
- Chen, C., Brodie, J.F., Kays, R., Davies, T.J., Liu, R., Fisher, J.T., Ahumada, J., McShea, W., Sheil, D., Agwanda, B., Andrianarisoa, M.H., Appleton, R.D., Bitariho, R., Espinosa, S., Grigione, M.M., Helgen, K.M., Hubbard, A., Hurtado, C.M., Jansen, P.A., Jiang, X., Jones, A., Kalies, E.L., Kiebou-Opepa, C., Li, X., Lima, M.G.M., Meyer, E., Miller, A.B., Murphy, T., Piana, R., Quan, R., Rota, C.T., Rovero, F., Santos, F., Schuttler, S., Uduman, A., Bommel, J.K., Young, H. & Burton, A.C. (2022). Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity. *CONSERVATION LETTERS*.
- Child, F.M., Roxburgh, L., Do Linh San, E., Raimondo, D. & Davies-Mostert, H.T. (2016). The red list of mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa. <[www.ewt.org.za](http://www.ewt.org.za)>.
- Chowdhury, S., Brown, J. & Swedell, L. (2020). Anthropogenic effects on the physiology and behaviour of chacma baboons in the Cape Peninsula of South Africa. *Conservation Physiology*, 8, coaa066.
- Convention on Biological Diversity. (2022). COP15: Nations Adopt Four Goals, 23 Targets for 2030 In Landmark UN Biodiversity Agreement [WWW Document]. Convention on Biological Diversity. URL <https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022>
- Cordier, C.P., Ehlers Smith, D.A., Ehlers Smith, Y. & Downs, C.T. (2022). Camera trap research in Africa: A systematic review to show trends in wildlife monitoring and its value as a research tool. *Global Ecology and Conservation*, 40, e02326.
- Corlett, R.T. (2015). The Anthropocene concept in ecology and conservation. *Trends in Ecology & Evolution*, 30, 36–41.
- Cox, D.T.C., Gardner, A.S. & Gaston, K.J. (2021). Diel niche variation in mammals associated with expanded trait space. *Nat Commun*, 12, 1753.
- Craigie, I.D., Baillie, J.E.M., Balmford, A., Carbone, C., Collen, B., Green, R.E. & Hutton, J.M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143, 2221–2228.
- Crisp, A.G. (2015). Development role players' knowledge of ecological infrastructure in Eden district, South Africa.
- Crist, E., Mora, C. & Engelman, R. (2017). The interaction of human population, food production, and biodiversity protection. *Science*, 356, 260–264.

- Crutzen, P.J. (2002). Geology of mankind *The Anthropocene*, 1.
- Darimont, C.T., Fox, C.H., Bryan, H.M. & Reimchen, T.E. (2015). The unique ecology of human predators. *Science*, 349, 858–860.
- Diaz, S. (2019). Pervasive human-driven decline of life on Earth points to the need for profound change. *Science*, 331, 341–346.
- digiKam Team. (2001). DigiKam [Computer software].
- Ditmer, M.A., Stoner, D.C., Francis, C.D., Barber, J.R., Forester, J.D., Choate, D.M., Ironside, K.E., Longshore, K.M., Hersey, K.R., Larsen, R.T., McMillan, B.R., Olson, D.D., Andreasen, A.M., Beckmann, J.P., Holton, P.B., Messmer, T.A. & Carter, N.H. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore. *Ecography*, 44, 149–161.
- Do Linh San, E., Mbatyoti, O.A., Palmer, G., Stuart, C., Stuart, M., Avenant, N.L. & Cavallini, P. (2016). A conservation assessment of *Herpestes pulverulentus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, DaviesMostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 1.
- Do Linh San, E., Nqinana, A., Madikiza, Z.J. & Somers, M.J. (2020). Diet of the marsh mongoose around a non-permanent reservoir: response of a generalist opportunist forager to the absence of crabs. *African Zoology*, 55, 240–244.
- Doherty, T.S., Dickman, C.R., Johnson, C.N., Legge, S.M., Ritchie, E.G. & Woinarski, J.C.Z. (2017). Impacts and management of feral cats *Felis catus* in Australia. *Mammal Review*, 47, 83–97.
- Doherty, T.S., Hays, G.C. & Driscoll, D.A. (2021). Human disturbance causes widespread disruption of animal movement. *Nat Ecol Evol*, 5, 513–519.
- Dominoni, D.M., Borniger, J.C. & Nelson, R.J. (2016). Light at night, clocks and health: from humans to wild organisms. *Biology Letters*, 12, 20160015.
- Donaldson, S. & Kimlicka, D. (2011). *Zoopolis: A Political Theory of Animal Rights*.
- Downs, C.T., Alexander, J., Brown, M., Chibesa, M., Ehlers Smith, Y.C., Gumede, S.T., Hart, L., Josiah, K.K., Kalle, R., Maphalala, M., Maseko, M., McPherson, S., Ngcobo, S.P., Patterson, L., Pillay, K., Price, C., Raji, I.A., Ramesh, T., Schmidt, W., Senoge, N.D., Shivambu, T.C., Shivambu, N., Singh, N., Singh, P., Streicher, J., Thabethe, V., Thatcher, H., Widdows, C., Wilson, A.-L., Zungu, M.M. & Ehlers Smith, D.A. (2021). Modification of the third phase in the framework for vertebrate species persistence in urban mosaic environments. *Ambio*, 50, 1866–1878.
- Drouilly, M., Nattrass, N. & O’Riain, M.J. (2018). Dietary niche relationships among predators on farmland and a protected area: Diet of Predators on Contrasting Land Uses. *Jour. Wild. Mgmt.*, 82, 507–518.

- Dyck, H.V. (2012). Changing organisms in rapidly changing anthropogenic landscapes: the significance of the 'Umwelt'-concept and functional habitat for animal conservation. *Evolutionary Applications*, 5, 144–153.
- Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, 19, 589–606.
- Ergete, E.A., Hailemariam, T.W., Balakrishnan, M. & Serfass, T.L. (2018). Fishermen knowledge and conflict with African clawless otters in and around Lake Tana, Ethiopia. *Afr. J. Ecol.*, 56, 409–413.
- Fagerholm, N., Martín-López, B., Torralba, M., Oteros-Rozas, E., Lechner, A.M., Bieling, C., Stahl Olafsson, A., Albert, C., Raymond, C.M., Garcia-Martin, M., Gulsrud, N. & Plieninger, T. (2020). Perceived contributions of multifunctional landscapes to human well-being: Evidence from 13 European sites. *People and Nature*, 2, 217–234.
- Fahrig, L., Watling, J.I., Arnillas, C.A., Arroyo-Rodríguez, V., Jörger-Hickfang, T., Müller, J., Pereira, H.M., Riva, F., Rösch, V., Seibold, S., Tscharntke, T. & May, F. (2022). Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biological Reviews*, 97, 99–114.
- Fauna & Flora International. (2021). Coordinated and collaborative application of the mitigation hierarchy in complex multi-use landscapes in Africa. A conceptual framework integrating socioecological considerations. FFI: Cambridge U.K. Available from: [www.fauna-flora.org](http://www.fauna-flora.org).
- Faure, J.P.B., Swanepoel, L.H., Cilliers, D., Venter, J.A. & Hill, R.A. (2021). Estimates of carnivore densities in a human-dominated agricultural matrix in South Africa. *Oryx*, 1–8.
- Ferreira, A.S., Peres, C.A., Bogoni, J.A. & Cassano, C.R. (2018). Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. *Mam Rev*, 48, 312–327.
- Fischer, J., Gardner, T.A., Bennett, E.M., Balvanera, P., Biggs, R., Carpenter, S., Daw, T., Folke, C., Hill, R., Hughes, T.P., Luthe, T., Maass, M., Meacham, M., Norström, A.V., Peterson, G., Queiroz, C., Seppelt, R., Spierenburg, M. & Tenhunen, J. (2015). Advancing sustainability through mainstreaming a social–ecological systems perspective. *Current Opinion in Environmental Sustainability*, 14, 144–149.
- Fischer, J. & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, 16, 265–280.
- Fischer, J., Meacham, M. & Queiroz, C. (2017). A plea for multifunctional landscapes. *Frontiers in Ecology and the Environment*, 15, 59–59.
- Fleming, P.A. & Bateman, P.W. (2018). Novel predation opportunities in anthropogenic landscapes. *Animal Behaviour*, 138, 145–155.
- FNE. (2022). Bouquetins du Bary : l'inacceptable abattage d'une espèce protégée [WWW Document]. France Nature Environnement. URL <https://fne.asso.fr/communique-presse/bouquetins-du-bary-l-inacceptable-abattage-d-une-espece-protgee>

- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005). Global Consequences of Land Use. *Science*, 309, 570–574.
- Folke, C., Polasky, S., Rockström, J., Galaz, V., Westley, F., Lamont, M., Scheffer, M., Österblom, H., Carpenter, S.R., Chapin, F.S., Seto, K.C., Weber, E.U., Crona, B.I., Daily, G.C., Dasgupta, P., Gaffney, O., Gordon, L.J., Hoff, H., Levin, S.A., Lubchenco, J., Steffen, W. & Walker, B.H. (2021). Our future in the Anthropocene biosphere. *Ambio*, 50, 834–869.
- François-Xavier Fauvelle. (2006). *Histoire de l'Afrique du Sud. L'Univers historique*. Le Seuil.
- Frey, S., Volpe, J.P., Heim, N.A., Paczkowski, J. & Fisher, J.T. (2020). Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. *Oikos*, 129, 1128–1140.
- Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, 360, 1232–1235.
- Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M. & Burgess, N.D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation*, 161, 230–238.
- Geldmann, J., Manica, A., Burgess, N.D., Coad, L. & Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc Natl Acad Sci USA*, 116, 23209–23215.
- Ghoddousi, A., Buchholtz, E.K., Dietsch, A.M., Williamson, M.A., Sharma, S., Balkenhol, N., Kuemmerle, T. & Dutta, T. (2021). Anthropogenic resistance: accounting for human behavior in wildlife connectivity planning. *One Earth*, 4, 39–48.
- Gil, D. & Brumm, H. (2014). *Avian Urban Ecology*. Oxford University Press.
- Gilbert, N.A., McGinn, K.A., Nunes, L.A., Shipley, A.A., Bernath-Plaisted, J., Clare, J.D.J., Murphy, P.W., Keyser, S.R., Thompson, K.L., Maresh Nelson, S.B., Cohen, J.M., Widick, I.V., Bartel, S.L., Orrock, J.L. & Zuckerberg, B. (2022a). Daily activity timing in the Anthropocene. *Trends in Ecology & Evolution*, S0169534722002750.
- Gilbert, N.A., Stenglein, J.L., Pauli, J.N. & Zuckerberg, B. (2022b). Human disturbance compresses the spatiotemporal niche. *Proc. Natl. Acad. Sci. U.S.A.*, 119, e2206339119.
- Godet, L. & Devictor, V. (2018). What Conservation Does. *Trends in Ecology & Evolution*, 33, 720–730.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005). Farming and the Fate of Wild Nature. *Science*, 307, 550–555.
- Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y.M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E. & Milo, R. (2023). The global biomass of wild mammals. *Proc. Natl. Acad. Sci. U.S.A.*, 120, e2204892120.

- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. & Briggs, J.M. (2008). Global Change and the Ecology of Cities. *Science*, 319, 756–760.
- Guerbois, C., Chapanda, E. & Fritz, H. (2012). Combining multi-scale socio-ecological approaches to understand the susceptibility of subsistence farmers to elephant crop raiding on the edge of a protected area. *Journal of Applied Ecology*, 49, 1149–1158.
- Haberl, H., Erb, K.H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., Gingrich, S., Lucht, W. & Fischer-Kowalski, M. (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proc. Natl. Acad. Sci. U.S.A.*, 104, 12942–12947.
- Hale, R. & Swearer, S.E. (2016). Ecological traps: current evidence and future directions. *Proc Biol Sci*, 283, 20152647.
- Hanekom, N. & Randall, R.M. (2015). Assessments of occurrence and distribution of mammals in forests of the Garden Route National Park based on camera trapping. *Koedoe*, 57, a1257.
- Hanks, J. (2003). Transfrontier Conservation Areas (TFCAs) in Southern Africa: Their Role in Conserving Biodiversity, Socioeconomic Development and Promoting a Culture of Peace. *Journal of Sustainable Forestry*, 17, 127–148.
- Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H.M., Dias, M.P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N.J.B., Iversen, L.L., Outhwaite, C.L., Visconti, P. & Geldmann, J. (2021). Using the IUCN Red List to map threats to terrestrial vertebrates at global scale. *Nat Ecol Evol*, 5, 1510–1519.
- Hill, S.L.L., Gonzalez, R., Sanchez-Ortiz, K., Caton, E., Espinoza, F., Newbold, T., Tylianakis, J., Scharlemann, J.P.W., De Palma, A. & Purvis, A. (2018). Worldwide impacts of past and projected future land-use change on local species richness and the Biodiversity Intactness Index (preprint). *Ecology*.
- Hobbs, R.J., Higgs, E. & Harris, J.A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution*, 24, 599–605.
- Hoffman, M., Koenig, K., Bunting, G., Costanza, J. & Williams, K.J. (2016a). Biodiversity Hotspots (version 2016.1).
- Hoffman, T., Beamish, E., Kaplan, B., Lewis, M., O'Riain, M.J., Sithaldeen, R. & Stone, O. (2016b). A conservation assessment of *Papio ursinus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Hoffman, T.S. & O'Riain, M.J. (2012). Landscape requirements of a primate population in a human-dominated environment. *Front Zool*, 9, 1.
- Hofmeester, T.R., Cromsigt, J.P.G.M., Odden, J., Andrén, H., Kindberg, J. & Linnell, J.D.C. (2019). Framing pictures: A conceptual framework to identify and correct for biases in detection

probability of camera traps enabling multi-species comparison. *Ecology and Evolution*, 9, 2320–2336.

Hollings, T., Jones, M., Mooney, N. & McCallum, H. (2013). Wildlife disease ecology in changing landscapes: Mesopredator release and toxoplasmosis. *International Journal for Parasitology: Parasites and Wildlife*, 2, 110–118.

Hulme-Beaman, A., Dobney, K., Cucchi, T. & Searle, J.B. (2016). An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments. *Trends in Ecology & Evolution*, 31, 633–645.

Iglesias-Carrasco, M., Aich, U., Jennions, M.D. & Head, M.L. (2020). Stress in the city: meta-analysis indicates no overall evidence for stress in urban vertebrates. *Proc. R. Soc. B.*, 287, 20201754.

Inskip, C. & Zimmermann, A. (2009). Human-felid conflict: a review of patterns and priorities worldwide. *ORX*, 43, 18.

IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Zenodo.

Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: a question of evolving, acclimatizing or coping with urban environmental stress. *Funct Ecol*, 29, 913–923.

IUCN. (2022). The IUCN Red List of Threatened Species. Version 2022-2. <https://www.iucnredlist.org>. Accessed on 10 February 2023.

Jacques, H., Reed-Smith, J. & Somers, M.J. (2014). *Aonyx capensis*: The IUCN Red List of Threatened Species 2015: e.T1793A21938767.

Jansen, C., Leslie, A.J., Cristescu, B., Teichman, K.J. & Martins, Q. (2019). Determining the diet of an African mesocarnivore, the caracal: scat or GPS cluster analysis? *Wildlife Biology*, 2019.

Jansen van Vuuren, A., Fritz, H. & Venter, J.A. (2022). Five small antelope species diets indicate different levels of anthrodependence in the Overberg Renosterveld, South Africa. *African Journal of Ecology*, n/a.

Jenner, L. (2018). Garden Route Fires in South Africa Continue to Devastate [WWW Document]. NASA. URL <http://www.nasa.gov/image-feature/goddard/2018/garden-route-fires-in-south-africa-continue-to-devastate>

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M. & Purvis, A. (2009). PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648–2648.

Jones-Walters, L. (2008). Biodiversity in multifunctional landscapes. *Journal for Nature Conservation*, 16, 117–119.

- Jordan, N.R., Smith, B.P., Appleby, R.G., Eeden, L.M. & Webster, H.S. (2020). Addressing inequality and intolerance in human–wildlife coexistence. *Conservation Biology*, 34, 803–810.
- Kansky, R., Kidd, M. & Fischer, J. (2021). Understanding drivers of human tolerance towards mammals in a mixed-use transfrontier conservation area in southern Africa. *Biological Conservation*, 254, 108947.
- Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R. & Kumar, N.S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proc. R. Soc. B.*, 284, 20161860.
- Kareiva, P. & Marvier, M. (2012). What Is Conservation Science? *BioScience*, 62, 962–969.
- Kays, R., Arbogast, B.S., Baker-Whitton, M., Beirne, C., Boone, H.M., Bowler, M., Burneo, S.F., Cove, M.V., Ding, P., Espinosa, S., Gonçalves, A.L.S., Hansen, C.P., Jansen, P.A., Kolowski, J.M., Knowles, T.W., Lima, M.G.M., Millsbaugh, J., McShea, W.J., Pacifici, K., Parsons, A.W., Pease, B.S., Rovero, F., Santos, F., Schuttler, S.G., Sheil, D., Si, X., Snider, M. & Spironello, W.R. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, 11, 700–713.
- Krief, S., Berny, P., Gumisiriza, F., Gross, R., Demeneix, B., Fini, J.B., Chapman, C.A., Chapman, L.J., Seguya, A. & Wasswa, J. (2017). Agricultural expansion as risk to endangered wildlife: Pesticide exposure in wild chimpanzees and baboons displaying facial dysplasia. *Science of The Total Environment*, 598, 647–656.
- Krief, S., Iglesias-González, A., Appenzeller, B.M.R., Rachid, L., Beltrame, M., Asalu, E., Okimat, J.-P., Kane-Maguire, N. & Spirhanzlova, P. (2022). Chimpanzee exposure to pollution revealed by human biomonitoring approaches. *Ecotoxicology and Environmental Safety*, 233, 113341.
- Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., De Palma, A., DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A.M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A.J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W. & Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 585, 551–556.
- Leighton, G.R.M., Bishop, J.M., Camarero, P.R., Mateo, R., O’Riain, M.J. & Serieys, L.E.K. (2022a). Poisoned chalice: Use of transformed landscapes associated with increased persistent organic pollutant concentrations and potential immune effects for an adaptable carnivore. *Science of The Total Environment*, 822, 153581.
- Leighton, G.R.M., Bishop, J.M., Merondun, J., Winterton, D.J., O’Riain, M.J. & Serieys, L.E.K. (2022b). Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. *Animal Conservation*, 25, 244–258.

- Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56–64.
- Levy, O., Dayan, T., Porter, W.P. & Kronfeld-Schor, N. (2019). Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecol Monogr*, 89, e01334.
- Lindsey, P.A., Chapron, G., Petracca, L.S., Burnham, D., Hayward, M.W., Henschel, P., Hinks, A.E., Garnett, S.T., Macdonald, D.W., Macdonald, E.A., Ripple, W.J., Zander, K. & Dickman, A. (2017a). Relative efforts of countries to conserve world's megafauna. *Global Ecology and Conservation*, 10, 243–252.
- Lindsey, P.A., Petracca, L.S., Funston, P.J., Bauer, H., Dickman, A., Everatt, K., Flyman, M., Henschel, P., Hinks, A.E., Kasiki, S., Loveridge, A., Macdonald, D.W., Mandisodza, R., Mgoola, W., Miller, S.M., Nazerali, S., Siegel, L., Uiseb, K. & Hunter, L.T.B. (2017b). The performance of African protected areas for lions and their prey. *Biological Conservation*, 209, 137–149.
- Locke, H., Rockström, J., Bakker, P., Bapna, M., Gough, M., Lambertini, M., Morris, J., Polman, P., Samper, C., Sanjayan, M., Zabey, E. & Zurita, P. (2021). A Nature-Positive World: The Global Goal for Nature.
- Loh, J., Green, R.E., Ricketts, T., Lamoreux, J., Jenkins, M., Kapos, V. & Randers, J. (2005). The Living Planet Index: using species population time series to track trends in biodiversity. *Phil. Trans. R. Soc. B*, 360, 289–295.
- Louvrier, J.L.P., Planillo, A., Stillfried, M., Hagen, R., Börner, K., Kimmig, S., Ortmann, S., Schumann, A., Brandt, M. & Kramer-Schadt, S. (2021). Spatiotemporal interactions of a novel mesocarnivore community in an urban environment before and during SARS-CoV-2 lockdown. *Journal of Animal Ecology*, 91, 367–380.
- Lovell, S.T. & Johnston, D.M. (2009). Creating multifunctional landscapes: how can the field of ecology inform the design of the landscape? *Frontiers in Ecology and the Environment*, 7, 212–220.
- Loveridge, A.J., Kuiper, T., Parry, R.H., Sibanda, L., Hunt, J.H., Stapelkamp, B., Sebele, L. & Macdonald, D.W. (2017). Bells, bomas and beefsteak: complex patterns of human-predator conflict at the wildlife-agropastoral interface in Zimbabwe. *PeerJ*, 5, e2898.
- Mace, G.M. (2014). Whose conservation? *Science*, 345, 1558–1560.
- Maclagan, S.J., Coates, T. & Ritchie, E.G. (2018). Don't judge habitat on its novelty: Assessing the value of novel habitats for an endangered mammal in a peri-urban landscape. *Biological Conservation*, 223, 11–18.
- Marchand, P., Freycon, P., Herbaux, J.-P., Game, Y., Toïgo, C., Gilot-Fromont, E., Rossi, S. & Hars, J. (2017). Sociospatial structure explains marked variation in brucellosis seroprevalence in an Alpine ibex population. *Sci Rep*, 7, 15592.
- Marchese, C. (2015). Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation*, 3, 297–309.

- Margaret W. Wilson, April D. Ridlon, Kaitlyn M. Gaynor, Steven D. Gaines, Adrian C. Stier, & Benjamin S. Halpern. (2020). Ecological impacts of human-induced animal behaviour change, 1522–1536.
- Mariki, S.B., Svarstad, H. & Benjaminsen, T.A. (2015). Elephants over the Cliff: Explaining Wildlife Killings in Tanzania. *Land Use Policy*, 44, 19–30.
- Martin, J.-L., Maris, V. & Simberloff, D.S. (2016). The need to respect nature and its limits challenges society and conservation science. *Proc. Natl. Acad. Sci. U.S.A.*, 113, 6105–6112.
- Martins, Q., Horsnell, W.G.C., Titus, W., Rautenbach, T. & Harris, S. (2011). Diet determination of the Cape Mountain leopards using global positioning system location clusters and scat analysis: Leopard diet determination by GPS and scat analysis. *Journal of Zoology*, 283, 81–87.
- Maseko, M., Zungu, M., Ehlers Smith, D., Ehlers Smith, Y. & Downs, C. (2020). Effects of habitat-patch size and patch isolation on the diversity of forest birds in the urban-forest mosaic of Durban, South Africa. *Urban Ecosystems*, 23.
- Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S.L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O. & Watson, J.E.M. (2020). Area-based conservation in the twenty-first century. *Nature*, 586, 217–227.
- Mazue, F., Guerbois, C., Fritz, H., Rebut, N. & Petit, O. (2023). Less bins, less baboons: reducing access to anthropogenic food effectively decreases the urban foraging behavior of a troop of chacma baboons (*Papio hamadryas ursinus*) in a peri-urban area. *Primates*, 64, 91–103.
- McInturff, A., Cannon, C.E.B., Alagona, P.S. & Pellow, D.N. (2021). Meeting at the crossroads: An environmental justice framework for large carnivore reintroductions and recoveries. *Elementa: Science of the Anthropocene*, 9, 00172.
- McKee, J.K., Sciulli, P.W., Foose, C.D. & Waite, T.A. (2004). Forecasting global biodiversity threats associated with human population growth. *Biological Conservation*, 115, 161–164.
- McPherson, S.C., Brown, M. & Downs, C.T. (2016). Crowned eagle nest sites in an urban landscape: Requirements of a large eagle in the Durban Metropolitan Open Space System. *Landscape and Urban Planning*, 146, 43.
- McShane, T.O., Hirsch, P.D., Trung, T.C., Songorwa, A.N., Kinzig, A., Monteferri, B., Mutekanga, D., Thang, H.V., Dammert, J.L., Pulgar-Vidal, M., Welch-Devine, M., Peter Brosius, J., Coppolillo, P. & O'Connor, S. (2011). Hard choices: Making trade-offs between biodiversity conservation and human well-being. *Biological Conservation*, 144, 966–972.
- van der Meer, E., Fritz, H., Blinston, P. & Rasmussen, G.S.A. (2014). Ecological trap in the buffer zone of a protected area: effects of indirect anthropogenic mortality on the African wild dog *Lycaon pictus*. *Oryx*, 48, 285–293.
- Miguel, E., Grosbois, V., Fritz, H., Caron, A., de Garine-Wichatitsky, M., Nicod, F., Loveridge, A.J., Stapelkamp, B., Macdonald, D.W. & Valeix, M. (2017). Drivers of foot-and-mouth disease

- in cattle at wild/domestic interface: Insights from farmers, buffalo and lions. *Divers Distrib*, 23, 1018–1030.
- Mills, D.R., Do Linh San, E., Robinson, H., Isoke, S., Slotow, R. & Hunter, L. (2019). Competition and specialization in an African forest carnivore community. *Ecol Evol*, 9, 10092–10108.
- Milner-Gulland, E.J., Addison, P., Arlidge, W.N.S., Baker, J., Booth, H., Brooks, T., Bull, J.W., Burgass, M.J., Ekstrom, J., zu Ermgassen, S.O.S.E., Fleming, L.V., Grub, H.M.J., von Hase, A., Hoffmann, M., Hutton, J., Juffe-Bignoli, D., ten Kate, K., Kiesecker, J., Kümpel, N.F., Maron, M., Newing, H.S., Ole-Moiyoi, K., Sinclair, C., Sinclair, S., Starkey, M., Stuart, S.N., Tayleur, C. & Watson, J.E.M. (2021). Four steps for the Earth: mainstreaming the post-2020 global biodiversity framework. *One Earth*, 4, 75–87.
- Moll, R.J., Killion, A.K., Hayward, M.W. & Montgomery, R.A. (2021). A Framework for the Eltonian Niche of Humans. *BioScience*, 71, 928–941.
- Montgomery, R.A., Moll, R.J., Say-Sallaz, E., Valeix, M. & Prugh, L.R. (2019). A tendency to simplify complex systems. *Biological Conservation*, 233, 1–11.
- Moolman, L., Morney, M.A. de, Ferreira, S.M., Ganswindt, A., Poole, J.H. & Kerley, G.I.H. (2019). And Then There was One: A Camera Trap Survey of the Declining Population of African Elephants in Knysna, South Africa. *African Journal of Wildlife Research*, 49.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008). Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. *Science*, 322, 261–264.
- Murphy, A., Diefenbach, D.R., Terner, M., Lovallo, M. & Miller, D. (2021). Threading the needle: How humans influence predator–prey spatiotemporal interactions in a multiple-predator system. *Journal of Animal Ecology*, 90, 2377–2390.
- Murray, M.H., Sánchez, C.A., Becker, D.J., Byers, K.A., Worsley-Tonks, K.E. & Craft, M.E. (2019). City sicker? A meta-analysis of wildlife health and urbanization. *Frontiers in Ecology and the Environment*, 17, 575–583.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W. & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, 16, e2006841.
- Nickel, B.A., Suraci, J.P., Allen, M.L. & Wilmers, C.C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, 241, 108383.
- Niedballa, J., Wilting, A., Sollmann, R., Hofer, H. & Courtiol, A. (2019). Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. *Remote Sens Ecol Conserv*, 5, 272–285.

- Nielsen, J.M., Clare, E.L., Hayden, B., Brett, M.T. & Kratina, P. (2018). Diet tracing in ecology: Method comparison and selection. *Methods Ecol Evol*, 9, 278–291.
- Obura, D.O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoilys, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M. & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, 373, 746–748.
- O’Connell, A.F., Nichols, J.D., Karanth, K.U. & Royle, J.A. (2011). Camera trap in Ecology. In: *Camera Traps in Animal Ecology*. Springer Japan, Tokyo, pp. 163–190.
- O’Farrell, P.J. & Anderson, P.M. (2010). Sustainable multifunctional landscapes: a review to implementation. *Current Opinion in Environmental Sustainability*, 2, 59–65.
- Osner, N. (2022). TrapTagger [Computer software].
- Ostrom, E. (2007). A diagnostic approach for going beyond panaceas. *Proc. Natl. Acad. Sci. U.S.A.*, 104, 15181–15187.
- Palmer, M.S., Gaynor, K.M., Abraham, J.O. & Pringle, R.M. (2023). The role of humans in dynamic landscapes of fear. *Trends in Ecology & Evolution*, 38, 217–218.
- Palmer, M.S., Gaynor, K.M., Becker, J.A., Abraham, J.O., Mumma, M.A. & Pringle, R.M. (2022). Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends in Ecology & Evolution*, 37, 911–925.
- Pardo, L.E., Bombaci, S.P., Huebner, S., Somers, M.J., Fritz, H., Downs, C., Guthmann, A., Hetem, R.S., Keith, M., le Roux, A., Mqgatsa, N., Packer, C., Palmer, M.S., Parker, D.M., Peel, M., Slotow, R., Strauss, W.M., Swanepoel, L., Tambling, C., Tsie, N., Vermeulen, M., Willi, M., Jachowski, D.S. & Venter, J.A. (2021). Snapshot Safari: a large-scale collaborative to monitor Africa’s remarkable biodiversity. *S. Afr. J. Sci*, 117.
- Pardo, L.E., Campbell, M.J., Cove, M.V., Edwards, W., Clements, G.R. & Laurance, W.F. (2019). Land management strategies can increase oil palm plantation use by some terrestrial mammals in Colombia. *Sci Rep*, 9, 7812.
- Paschoal, A.M.O., Massara, R.L., Santos, J.L. & Chiarello, A.G. (2012). Is the domestic dog becoming an abundant species in the Atlantic forest? A study case in southeastern Brazil. *mammalia*, 76.
- Patterson, L., Kalle, R. & Downs, C. (2017). A citizen science survey: perceptions and attitudes of urban residents towards vervet monkeys. *Urban Ecosyst*, 20, 617–628.
- Patterson, L., Kalle, R. & Downs, C. (2018). Factors affecting presence of vervet monkey troops in a suburban matrix in KwaZulu-Natal, South Africa. *Landscape and Urban Planning*, 169, 220–228.
- Patterson, L., Kalle, R. & Downs, C.T. (2019). Living in the suburbs: Space use by vervet monkeys (*Chlorocebus pygerythrus*) in an eco-estate, South Africa. *African Journal of Ecology*, 57, 539–551.

- Pérez-Flores, J., Mardero, S., López-Cen, A. & Contreras-Moreno, F.M. (2021). Human-wildlife conflicts and drought in the greater Calakmul Region, Mexico: implications for tapir conservation. *Neotropical Biology and Conservation*, 16, 539–563.
- Pessoa, L. (2021). *Complex Systems: The Science of Interacting Parts*.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011). Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science*, 333, 1289–1291.
- Phillips, A. (2004). The history of the international system of protected areamanagement categories. *Parks*, 14, 4–14.
- Pienaar, L. (2020). *Agriculture in the Garden Route: Towards resilience post-COVID19*. Western Cape Government.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752.
- Pocock, M.J.O., Searle, J.B. & White, P.C.L. (2004). Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms: Population dynamics of commensal house mice. *Journal of Animal Ecology*, 73, 878–888.
- Pool-Stanvliet, R. & Coetzer, K. (2020). The scientific value of UNESCO biosphere reserves. *S. Afr. J. Sci.*, 116.
- Ramesh, T. & Downs, C.T. (2013). Impact of farmland use on population density and activity patterns of serval in South Africa. *J Mammal*, 94, 1460–1470.
- Ramesh, T., Kalle, R. & Downs, C.T. (2017). Space use in a South African agriculture landscape by the caracal (*Caracal caracal*). *Eur J Wildl Res*, 63, 11.
- Reyers, B., O'Farrell, P.J., Nel, J.L. & Wilson, K. (2012). Expanding the conservation toolbox: conservation planning of multifunctional landscapes. *Landscape Ecol*, 27, 1121–1134.
- Roberts, D.C. (1994). The Design of an Urban Open-space Network for the City of Durban (South Africa). *Envir. Conserv.*, 21, 11–17.
- Roberts, P.D., Somers, M.J., White, R.M. & Nel, J.A.J. (2007). Diet of the South African large-spotted genet *Genetta tigrina* (Carnivora, Viverridae) in a coastal dune forest. *Acta Theriol*, 52, 45–53.
- Rodary, E. (2019). *L'Apartheid et l'animal – Vers une politique de la connectivité*.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. & Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640–643.

- Rodrigues, A.S.L. & Cazalis, V. (2020). The multifaceted challenge of evaluating protected area effectiveness. *Nat Commun*, 11, 5147.
- Rosenzweig, M.L. (2003). Reconciliation ecology and the future of species diversity. *Oryx*, 37, 194–205.
- Rota, C.T., Ferreira, M.A.R., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. & Millspaugh, J.J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7, 1164–1173.
- Roux, D.J., Smith, M.K.S., Smit, I.P.J., Freitag, S., Slabbert, L., Mokhatla, M.M., Hayes, J. & Mpapane, N.P. (2020). Cultural ecosystem services as complex outcomes of people–nature interactions in protected areas. *Ecosystem Services*, 43, 101111.
- Russell W.M.S. & Burch. (1959). *The principles of humane experimental technique*.
- Saenz, S., Walschburger, T., González, J.C., León, J., McKenney, B. & Kiesecker, J. (2013). Development by Design in Colombia: Making Mitigation Decisions Consistent with Conservation Outcomes. *PLOS ONE*, 8, e81831.
- SANParks. (2020). *Garden Route National Park: Park Management Plan For the period 2020 - 2029*. Pretoria: Department of Environment, Forestry and Fisheries.
- Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A. & Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. *Ecology Letters*, 22, 365–376.
- Schell, C.J., Stanton, L.A., Young, J.K., Angeloni, L.M., Lambert, J.E., Breck, S.W. & Murray, M.H. (2021). The evolutionary consequences of human–wildlife conflict in cities. *Evolutionary Applications*, 14, 178–197.
- Schnetler, A.K., Radloff, F.G.T. & O’Riain, M.J. (2021). Medium and large mammal conservation in the City of Cape Town: factors influencing species richness in urban nature reserves. *Urban Ecosyst*, 24, 215–232.
- Scholte, P., Nchoutpouen, C., Palla, F. & Doumenge, C. (2022). More is not enough: Central Africa and the proposed 30% protected and conserved areas by 2030. *Oryx*, 56, 810–811.
- Scholte, P., Pays, O., Adam, S., Chardonnet, B., Fritz, H., Mamang, J., Prins, H.H.T., Renaud, P., Tadjou, P. & Moritz, M. (2021). Conservation overstretch and long-term decline of wildlife and tourism in the Central African savannas. *Conservation Biology*, [cobi.13860](https://doi.org/10.1111/cobi.13860).
- Serieys, L.E.K., Hammond-Aryee, K., Bishop, J., Broadfield, J., O’Riain, M.J. & van Helden, P.D. (2019). High Seroprevalence of *Toxoplasma gondii* in an Urban Caracal (*Caracal caracal*) Population in South Africa. *Journal of Wildlife Diseases*, 55, 951.
- Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W. & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biological Reviews*, 95, 1689–1705.

- Seymour, C.L., Simmons, R.E., Morling, F., George, S.T., Peters, K. & O’Riain, M.J. (2020). Caught on camera: The impacts of urban domestic cats on wild prey in an African city and neighbouring protected areas. *Global Ecology and Conservation*, 23, e01198.
- Soulé, M.E. (1985). What is Conservation Biology?, 35.
- Steffen, W., Grinevald, J., Crutzen, P. & McNeill, J. (2011). The Anthropocene: conceptual and historical perspectives. *Phil. Trans. R. Soc. A.*, 369, 842–867.
- Stenseth, N.C., Leirs, H., Skonhøft, A., Davis, S.A., Pech, R.P., Andreassen, H.P., Singleton, G.R., Lima, M., Machang’u, R.S., Makundi, R.H., Zhang, Z., Brown, P.R., Shi, D. & Wan, X. (2003). Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, 1, 367–375.
- Streicher, J.P., Ramesh, T. & Downs, C.T. (2020). Home range and core area utilisation of three co-existing mongoose species: large grey, water and white-tailed in the fragmented landscape of the KwaZulu-Natal Midlands, South Africa. *Mamm Biol*, 100, 273–283.
- Streicher, J.P., Ramesh, T. & Downs, C.T. (2021). An African urban mesocarnivore: Navigating the urban matrix of Durban, South Africa. *Global Ecology and Conservation*, 26, e01482.
- Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forrester, T., Green, A.M., Haight, J., Harris, N.C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P.E., Lewis, J.S., McInturff, A., McShea, W., Murphy, T.W., Palmer, M.S., Parsons, A., Parsons, M.A., Pendergast, M.E., Pekins, C., Prugh, L.R., Sager-Fradkin, K.A., Schuttler, S., Şekercioğlu, Ç.H., Shepherd, B., Whipple, L., Whittington, J., Wittemyer, G. & Wilmers, C.C. (2021). Disturbance type and species life history predict mammal responses to humans. *Glob Change Biol*, 27, 3718–3731.
- Swanepoel, L.H., Balme, G., Williams, S., Power, R.J., Snyman, A., Gaigher, I., Senekal, C., Martins, Q. & Child, M.F. (2016). A conservation assessment of *Panthera pardus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 13.
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, 546, 73–81.
- Tourangeau, W., Lamarque, M., Greenland-Smith, S. & Sherren, K. (2020). Beyond intrinsic: a call to combine scales on motivation and environmental values in wildlife and farmland conservation research. *Human Dimensions of Wildlife*, 1–15.
- Treves, A. & Bruskotter, J. (2014). Tolerance for Predatory Wildlife. *Science*, 344, 476–477.
- Trisos, C.H., Auerbach, J. & Katti, M. (2021). Decoloniality and anti-oppressive practices for a more ethical ecology. *Nat Ecol Evol*.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Moorter, B.V., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown,

- D., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., Mourão, G. de M., Morato, R.G., Morellet, N., Morrison, T.A., Díaz-Muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., de Paula, R.C., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G. & Zi, F. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, 6.
- UNEP-WCMC, IUCN & NGS. (2020). Protected Planet Report 2020. Cambridge UK; Gland, Switzerland; and Washington, D.C., USA.
- UNESCO. (2019a). The UNESCO MAB program in South Africa. Values generated through Biosphere Reserves.
- UNESCO. (2019b). Biosphere Reserves [WWW Document]. UNESCO. URL <https://en.unesco.org/biosphere>
- Van Scoyoc, A., Smith, J.A., Gaynor, K.M., Barker, K. & Brashares, J.S. (2023). The influence of human activity on predator–prey spatiotemporal overlap. *Journal of Animal Ecology*, 1365–2656.13892.
- Venter, J., Seydack, A., Ehlers Smith, Y., Uys, R. & Child, M.F. (2016a). A conservation assessment of *Philantomba monticola*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 9.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016b). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat Commun*, 7, 12558.
- Wang, Y., Allen, M.L. & Wilmers, C.C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation*, 190, 23–33.
- Weinzettel, J., Vačkář, D. & Medková, H. (2018). Human footprint in biodiversity hotspots. *Front Ecol Environ*, 16, 447–452.
- Western Cape Government. (2019). Socio-economic profile: Garden Route District Municipality.

- Widdows, C. & Downs, C.T. (2017). Genets in the city: community observations and perceptions of large-spotted genets (*Genetta tigrina*) in an urban environment. *Urban Ecosyst.*
- Widdows, C.D. & Downs, C.T. (2015). A genet drive-through: are large spotted genets using urban areas for “fast food”? a dietary analysis. *Urban Ecosyst*, 18, 907–920.
- Widdows, C.D., Roberts, P.D., Maddock, A.H., Carvalho, F., Gaubert, P. & Do Linh San, E. (2016). A conservation assessment of *Genetta tigrina*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa., 6.
- Williams, B.A., Venter, O., Allan, J.R., Atkinson, S.C., Rehbein, J.A., Ward, M., Di Marco, M., Grantham, H.S., Ervin, J., Goetz, S.J., Hansen, A.J., Jantz, P., Pillay, R., Rodríguez-Buritica, S., Supples, C., Virnig, A.L.S. & Watson, J.E.M. (2020a). Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems. *One Earth*, 3, 371–382.
- Williams, D.R., Balmford, A. & Wilcove, D.S. (2020b). The past and future role of conservation science in saving biodiversity. *CONSERVATION LETTERS*, e12720.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. *Ecology*, 95, 2027–2027.
- Wilson, M.W., Ridlon, A.D., Gaynor, K.M., Gaines, S.D., Stier, A.C. & Halpern, B.S. (2020). Ecological impacts of human-induced animal behaviour change. *Ecology letters*, 23, 1522–1536.
- Woodroffe, R., Hedges, S. & Durant, S.M. (2014). To Fence or Not to Fence. *Science*, 344, 46–48.
- Worldometers. (2023). World population, <<https://www.worldometers.info/world-population/>>.
- Worm, B. (2015). A most unusual (super)predator. *Science*, 349, 784–785.
- Worm, B. & Paine, R.T. (2016). Humans as a Hyperkeystone Species. *Trends in Ecology & Evolution*, 31, 600–607.
- Wright, H.L., Lake, I.R. & Dolman, P.M. (2012). Agriculture-a key element for conservation in the developing world: Agriculture in developing-world conservation. *Conservation Letters*, 5, 11–19.
- WWF. (2022). Living planet report. Building a nature-positive society.
- Yirga, G., De longh, H.H., Leirs, H., Gebrihiwot, K., Deckers, J. & Bauer, H. (2012). Adaptability of large carnivores to changing anthropogenic food sources: diet change of spotted hyena (*Crocuta crocuta*) during Christian fasting period in northern Ethiopia: Adaptability of large carnivores to changing anthropogenic food sources. *Journal of Animal Ecology*, 81, 1052–1055.

Zungu, M.M., Maseko, M.S.T., Kalle, R., Ramesh, T. & Downs, C.T. (2020a). Factors affecting the occupancy of forest mammals in an urban-forest mosaic in EThekweni Municipality, Durban, South Africa. *Urban Forestry & Urban Greening*, 48, 126562.

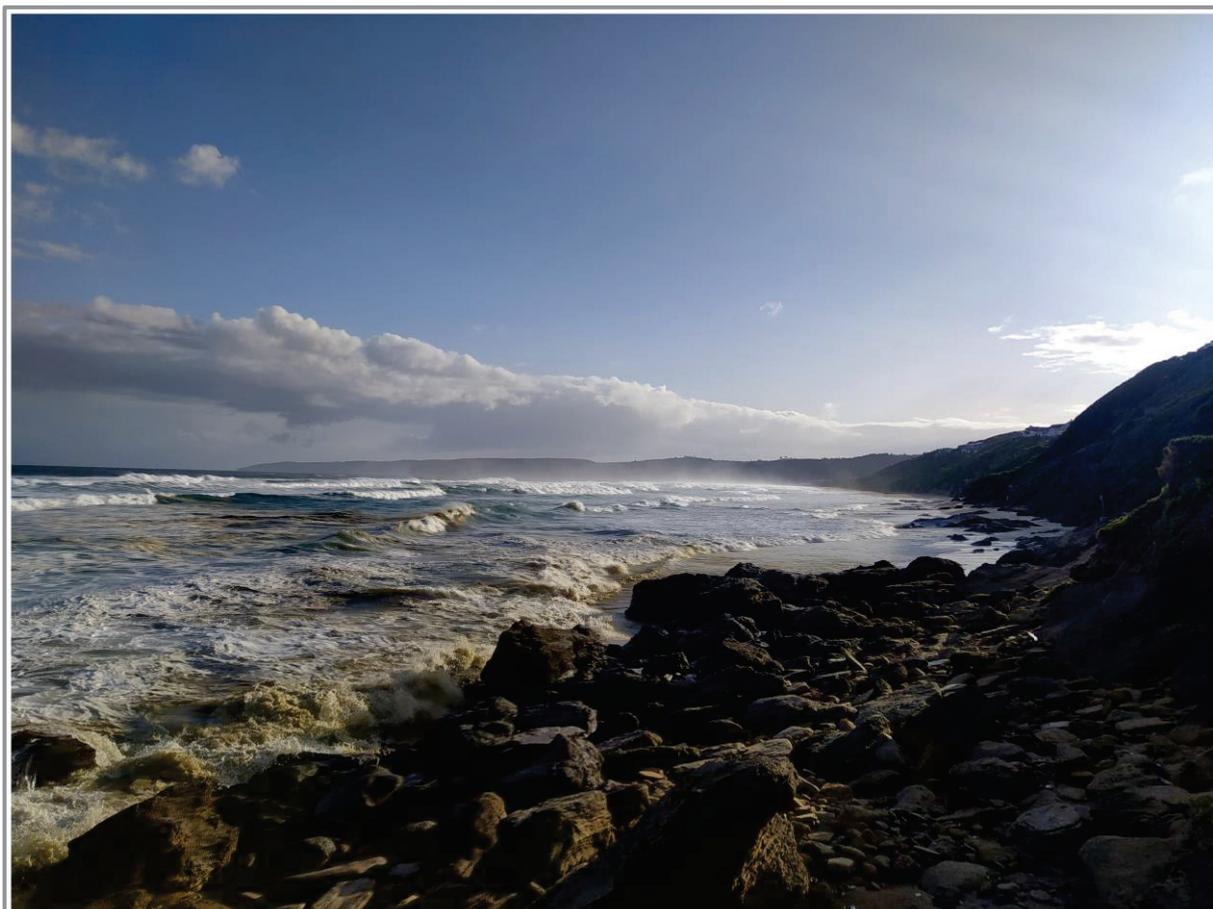
Zungu, M.M., Maseko, M.S.T., Kalle, R., Ramesh, T. & Downs, C.T. (2020b). Effects of landscape context on mammal richness in the urban forest mosaic of EThekweni Municipality, Durban, South Africa. *Global Ecology and Conservation*, 21, e00878.

Zwerts, J.A., Stephenson, P.J., Maisels, F., Rowcliffe, M., Astaras, C., Jansen, P.A., Waarde, J., Sterck, L.E.H.M., Verweij, P.A., Bruce, T., Brittain, S. & Kuijk, M. (2021). Methods for wildlife monitoring in tropical forests: Comparing human observations, camera traps, and passive acoustic sensors. *Conservat Sci and Prac*, 3.





# Appendices





## Appendix 1: Online survey

Questions	Choices
1. In which municipality do you live?	<i>Knysna; George; Bitou; Mossel Bay</i>
2. Please indicate the cell(s) where your property is located using the grid corresponding to your municipality	
3. The following species are known to be present in the Garden Route National Park. Please specify how regularly you have observed the presence of the following species on your property, over the past 3 years: (leave blank if you do not know)	<i>Blue duiker; Common duiker; Bushbuck; Grey rhebuck; Cape grysbok; Klipspringer; Steenbok; Bushpig; Aardvark; Elephant; Chacma baboon; Vervet monkey; Leopard; Caracal; African wildcat; Small-spotted genet; South African large-spotted genet; Genet (I cannot say which species); Large grey mongoose; Cape grey mongoose; Water mongoose; Mongoose (I cannot say which species); African clawless otter; Honey badger; African striped weasel; Striped polecat; Porcupine</i>
4. Which photograph shows a blue duiker?	
5. Which footprint corresponds to the caracal (the scale is on the left)?	<i>Large grey mongoose; Cape grey mongoose; Water mongoose; I am not sure</i>
6. Can you identify this species? The animal is 60 cm long.	
7. Are the following species occurring in your neighborhood (~1km around your property), over the past 3 years? (leave blank if you do not know)	
8. How do you know the following species are on your property?	<i>Feeding signs; Species carcasses; Camera traps; Someone told you; Sightings; Sounds; Tracks; Scats; Hair; Burrows; Other signs</i>
9. When are the following species present on your property?	<i>Early summer (Sept-Dec); Late summer (Jan-Apr); Winter (May- Aug); Throughout the year; Periodically (not seasonally); I do not know</i>
10. Do you have any further observations to share?	
11. As a local, would you say the presence of the following species on your property is:	<i>Decreasing; Stable; Increasing; I do not know</i>
12. How would you explain these changes (changes in land-uses, fires, floods...)? Do you have any further observations to share?	
13. What different habitats/vegetation can be found on your property and in which state?	<i>Fynbos; Degraded/regrowth fynbos; Thicket; Degraded/regrowth thicket; Afro temperate forest; Degraded/regrowth Afro temperate forest; Scrub forest; Degraded/regrowth scrub forest; Wetlands; Degraded/regrowth wetlands</i>
14. What different land use can be found on your property?	<i>Orchards; Vegetable garden; Pasture; Crops; Patches of exotic vegetation non-edible for humans (pine, black wattle, rooikrans); Other (please specify)</i>
15. What kind of water infrastructure can wild mammal species access on your property?	<i>Dam; Permanent watercourse; Temporary watercourse; Small pond; No water infrastructure; Other (please specify)</i>
16. Why do you have water infrastructures on your property? Leave blank if not applicable.	<i>For wildlife; For domestic animals; For other farming/gardening; It was there; Other (please specify)</i>
17. Do you compost your biodegradable waste?	<i>No; Yes, accessible to wild mammal species; Yes, not accessible to wild mammal species</i>
18. Do wild mammal species have access to your rubbish bags?	<i>No; Yes; Only on the day of rubbish pick-up</i>
19. Do you supply food to intentionally attract wild mammal species on your property?	<i>Yes; No</i>

20. Have any of these activities occurred on your property in the last 3 years?  
*Snaring; Hunting; Dog hunting; Poisoning; I do not know; I do not want to answer; None of these activities occurred on my property*
21. What domestic animals do you keep on your property? (Leave blank if not applicable)  
*Dogs; Cats; Horses; Donkeys; Poultry; Sheep; Goats; Cattle; Pigs; Rabbits; Bees; Fish; Other (please specify)*
22. If you ticked dogs, could you specify their number and breeds? If you don't have a dog, you can skip the following 4 questions.
23. Why do you have dog(s)?  
*Company; Protect the house from burglars; Protect the house from wild mammals, Hunting; Breeding, Other (please specify)*
24. Do your dogs walk alone on your property?
25. Have your dogs ever killed or injured a wild mammal species? If yes, how many times has this happened and which species were affected?
26. Have your cats ever killed or injured a wild mammal species? If yes, how many times has this happened and which species were affected? If you don't have a cat, you can skip the question.  
*Close to dam; close to river; in fynbos; in thicket; in afrotemperate or scrub forest; in wetlands; in riverine; in vegetable gardens; in orchards; in crops; in patches of exotic vegetation non edible for human; in pasture; close to human infrastructures*
27. Where do you most often notice the presence of the following species on your property?
28. If you have selected "other", could you please specify?
29. If you experienced any wild mammal related damage, injuries or loss on your property, what was affected? Leave blank if you have not experienced any damage.
30. Could you please give me a few examples of wild mammal species related damages on your property (ex. Baboons steal my tomatoes)?
31. What do you do to prevent this kind of damage?
32. Whose scat is the following photograph?
33. Do you have fences on your property?  
*Yes; Yes, partially; No*
34. Why is your property fenced?  
*Prevent criminality; Keep domestic animals in; Keep wild mammal species out; Crops/vegetables protection; It was there; Other (please specify)*
35. Which proportion of your property totally excludes wild mammal species?
36. Which proportion of your property is devoted exclusively to wild mammal species?
37. Which proportion of your property totally excludes your dogs?
38. Have you ever had a wild mammal trapped/killed in your fences? Which species was it and how often does it happen?
39. How many wild mammal species have you seen killed by road collisions in your neighborhood (~1km around your property)? Which species was affected?
40. For how long have you been living there?
41. What is your main reason for living here?  
Please select only one answer.  
*Born here; Family; Business; Employment; Facilities; Lifestyle; Proximity to nature; Other (please specify)*
42. In few words, could you describe what this property means for you?
43. What is the size of your property (ha)?  
*Principal residence; Commercial farming; Subsistence farming; Home gardening; Hospitality; Forestry; Game reserve; Holiday residence; I would rather not say; Other (please specify)*
44. What are the main activities on your property?
45. On average, how many people are on your property every day?
46. Do you live within 2km of the Garden Route National Park?  
*Yes; No; I am not sure*
47. Do you live within 500m of the nearest Critical Biodiversity Area?  
*Yes; No; I am not sure*

- 
48. Have you intentionally transformed your property to create a safe space for wild mammal species?
49. Did you have any knowledge (history, plants, wildlife) of the area before you moved in? *Yes, a good knowledge; Yes, a medium knowledge; No*
50. How often do you visit the parks and the reserves of the Garden Route? *Several times per week; Several times per month; Several times per year; Once a year; Never*
51. What is your main reason for visiting the parks and reserves of the Garden Route? Please select only one answer. *For physical activity; For nature; For social outings; For my own balance; Other (please specify)*
52. Do you contribute to any conservation initiative? *No; Non-profit organisations (NPO); Non-governmental organisation (NGO); Conservancy, which one?*
53. From your point of view, how would you qualify your experiences with the species present in your area? *Good; Neutral; Bad*
54. According to you, what are the main challenges to protect wild mammal species in the Garden Route?
55. Why do you think it is important to conserve the ecosystem and landscapes of the Garden Route? *I am aware of the regulations related to wild mammal species; I consider that I have a good knowledge of wild mammal species; Wild mammal species are beneficial for me from a monetary perspective; Wild mammal species are beneficial for me from a non-monetary perspective; I feel I have the technical capacity to deal with wild mammal species damage/loss on my property; I have the feeling I spend too much money preventing wild mammal species damage on my property; I have the feeling; I spend too much time preventing wild mammal species damage on my property; The needs of humans should take priority over wild mammal species protection; Wild mammal species are valuable only if people get to benefit from them in some way; It is essential to preserve wild mammal species for the role they play in the ecosystems; Wild mammal species must be protected regardless of their value to humans; I feel like it is my responsibility to protect wild mammal species; Wild mammal species contribute to the identity of the Garden Route; I would like to see more wild mammal species on my property; I would like to share more space on my property with mammal species; I would like to do more for the protection of wild mammal species in the Garden Route; I see the Garden Route National Park as an asset for my property; I see the Garden Route Biosphere Reserve as an asset for my property*
56. Do you 1) strongly agree, 2) agree, 3) neither agree nor disagree 4) disagree, 5) strongly disagree with the statements below?
57. How did you hear about this questionnaire? *Whatsapp; Facebook; E-mail address; From a friend; Other*
58. What motivated you to participate in this questionnaire?
59. Is there anything more you would like to add?
-



## Appendix 2: Supplementary information associated with chapter 1

As they are recording all day long. CTs can provide numerous information on wildlife activities. which were not addressed during this *PhD* thesis but could be interesting to investigate in the future.

### Appendix 2.1 Assess mammalian anthropogenic resources consumption with CTs data

The grid of CTs gave us some interesting hazard photographs of baboons and vervet monkeys stealing anthropogenic resources (Figure A2.1). It could be worthwhile to design a specific protocol to test whether it would be feasible to inform on the diet of mammals in the anthropogenic context from CTs.



**FIGURE A2.1:** Photographs from camera traps showing. A) vervet monkey with a corn cob stolen from a crop. B) vervet monkeys foraging in a pasture in Hoekwil and C) baboons with bananas and D) lemons stolen in a peri-urban area in Wilderness heights.

**Appendix 2.2 Document the predation from domestic animals with CTs data**

As documented by other studies, we detected cat predation on wildlife in the photographs (Doherty et al. 2017; Seymour et al. 2020). Moreover, we have not detected any predation by roaming or domestic dogs.



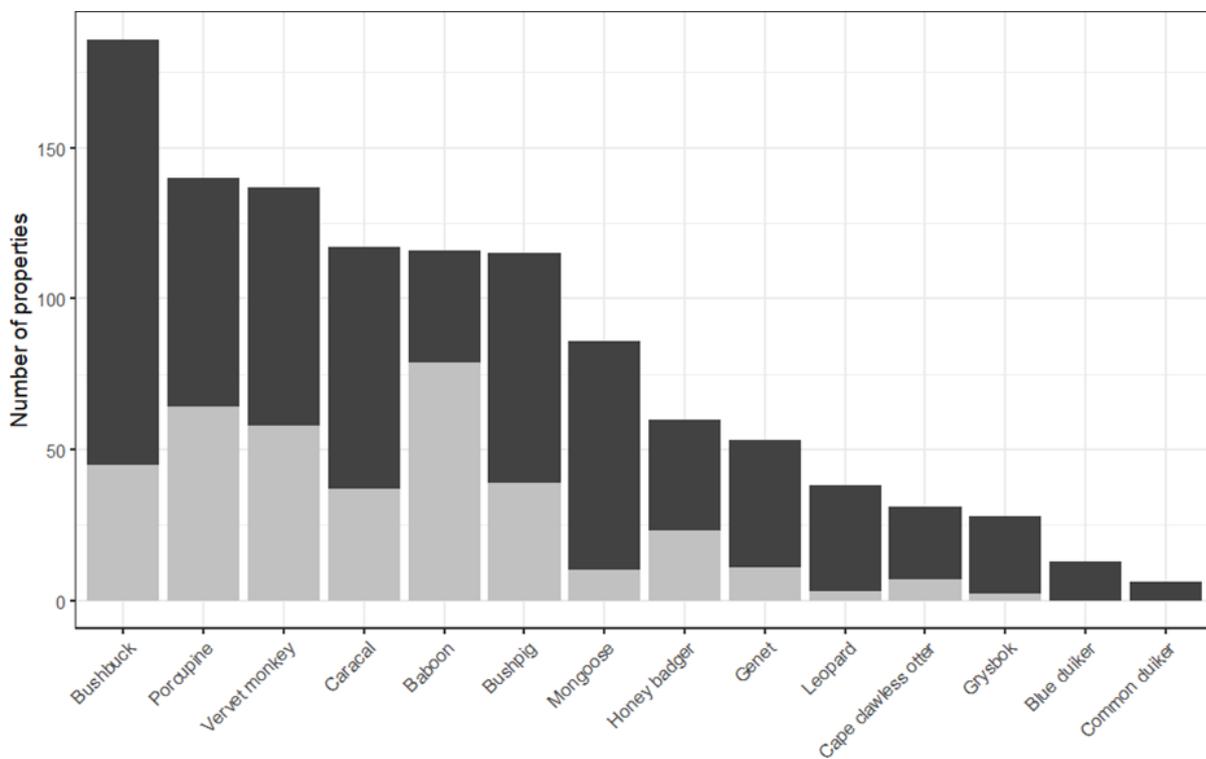
**FIGURE A2.2** Photographs from camera traps showing cats walking with their kill in two different peri-urban areas A) in Wilderness heights, the prey cannot be identified B) in Rheenendal, the prey could be a mole-rat.

## Appendix 3. Supplementary information associated with chapter 2

Some of the survey data were not used during this *PhD* thesis because of time constraints but could provide valuable results if analyzed in the future.

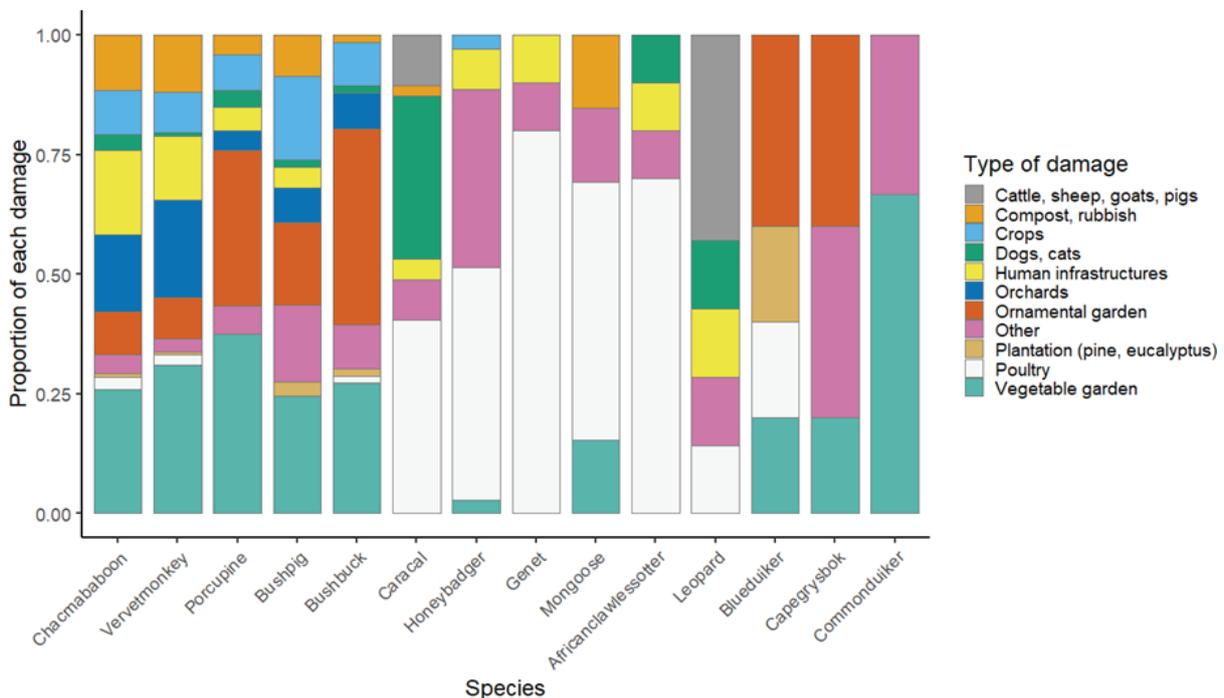
### Appendix 3.1 Assess mammalian anthropogenic resources consumption with survey data

Preliminary results from the survey provided some indications on mammals' damage, which can reflect their consumption of human food resources and could complement the information obtained with the CTs. Respondents were asked the following question: 'If you experienced any wild mammal related damage, injuries or loss on your property, what was affected?'. They had multiple choices for type of damages: livestock (cattle, sheep, goat, pig), compost/rubbish, crops, dogs/cats, human infrastructures, orchards, ornamental garden, plantation (pine, eucalyptus), poultry, vegetable garden. We calculated the number of properties that experienced at least one damage by a species and represented the type of damage that they selected (Figure A3.1). The baboon was the species responsible of the most damage, followed by the porcupine and the vervet monkey (Figure A3.1). Furthermore, most of the properties that reported the presence of baboons experienced damage (Figure A3.1).



**FIGURE A3.1:** Representation of the damage caused by species on respondents' properties. The dark grey bars represent the number of properties without damage and the light grey the properties with damage.

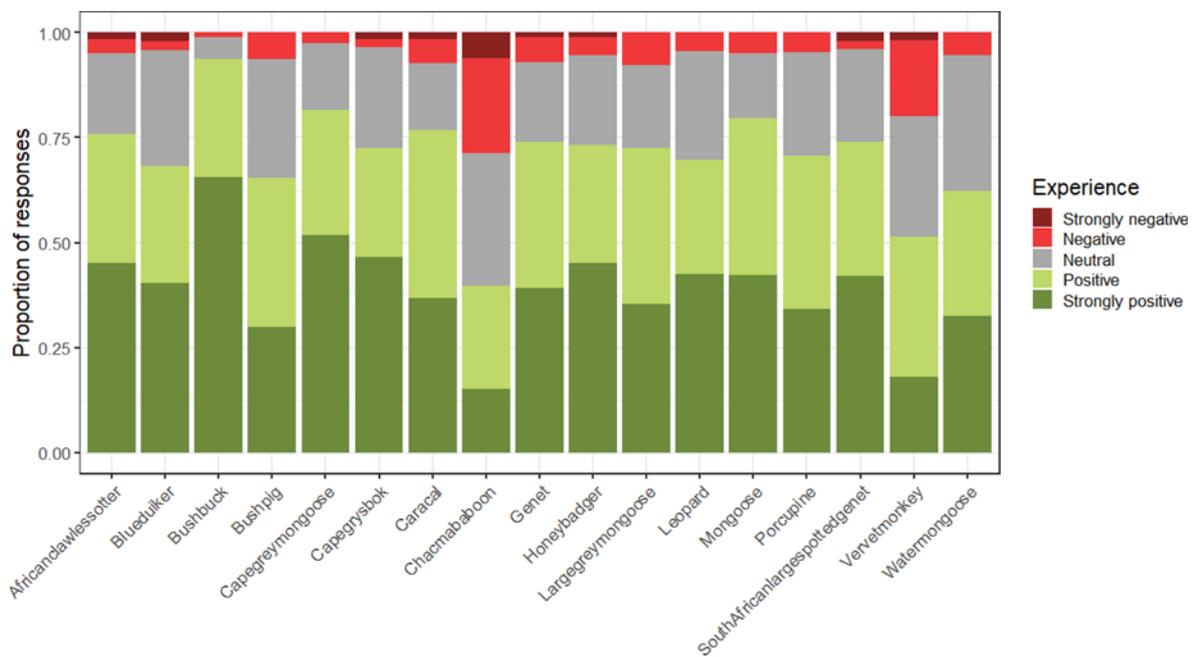
The type of damage was diverse, ranging from ornamental plants to livestock and domestic animals. Baboons and vervet monkeys had an impact on the largest diversity of categories, which seems consistent with their high diet flexibility (van Doorn et al. 2010). Carnivores mostly preyed on poultry (Figure A3.2). The results concerning the damage on poultry by the blue duiker are surprising, as they are herbivores and indicate that more in-depth analyses need to be performed (Figure A3.2). Baboons, vervet monkeys and porcupines were commonly detected with the survey and CTs. These results, in addition to photographs taken by the CTs (Figure A2.1), suggest that their success in anthropogenic landscapes may be linked to their capacity to benefit from the available food resources.



**FIGURE A3.2:** Responses represented per species to the question 'If you experienced any wild mammal related damage, injuries or loss on your property, what was affected?'. The colors represent the types of damage.

**Appendix 3.2 Document human experiences with wild mammals with survey data**

In the survey, respondents were also asked 'how would you qualify your experiences with the species present in your area?' and had the choices between 'strongly negative, negative, neutral, positive and strongly positive'. Preliminary results suggested that the experience with wildlife seemed overall positive with all species (Figure A3.3). However, primates (baboon and vervet monkey), concentrated the most of negative experiences followed by the bushpig, porcupine, caracal, genet and mongooses.



**FIGURE A.3.3:** Representation of the proportion of respondents experiencing strongly negative, negative, neutral, positive or strongly positive interactions with the various mammalian species.





# Résumé

## **Utilisation spatio-temporelle des paysages anthropisés multifonctionnels par les mammifères africains. Tester le principe d'anthropodépendance.**

La biodiversité mondiale subit une sixième extinction de masse principalement à cause des activités humaines. Elle ne pourra être préservée en protégeant seulement 30% de la surface terrestre, comme le prévoient les objectifs de la COP15. Des chercheurs proposent de créer des territoires partagés entre humains et espèces sauvages pour assurer la connectivité entre les aires protégées et reconnecter humains et nature (« Shared Earth »). Pour cela, il est nécessaire de savoir quels mammifères sauvages peuvent utiliser les habitats modifiés par les humains, comment le font-ils, et quels traits d'histoire de vie leur permettent de tirer avantage de ces nouveaux environnements. En effet, le modèle conceptuel sur l'anthropodépendance prédit des utilisations de l'espace et des ressources anthropiques variables en fonction des espèces. Les comportements spatio-temporels des mammifères sauvages présents dans la réserve de biosphère de la Garden Route, un paysage multifonctionnel en Afrique du Sud, ont été suivis grâce à des pièges photographiques et un questionnaire en ligne. Combiner ces méthodes permet d'obtenir des informations complémentaires, d'augmenter la couverture spatiale et le nombre de données, tout en impliquant diverses parties prenantes dans le processus de conservation. L'utilisation du territoire anthropisé ainsi que la tolérance des mammifères vis-à-vis des perturbations d'origine humaine (directes ou structurelles) se sont avérées dépendantes des espèces, témoignant de la diversité des stratégies développées par celles-ci. L'évitement temporel des humains semble cependant être la stratégie la plus répandue. Les zones fortement modifiées par l'homme semblent être plus favorables aux espèces de petites tailles et aux espèces avec un régime alimentaire généraliste plutôt qu'aux carnivores strictes. La préservation d'habitats naturels dans les territoires anthropisés, pour laquelle les initiatives privées sont fondamentales, permet à certains mammifères d'utiliser ces espaces, ce qui en fait un atout pour la conservation de certaines espèces, en appui aux aires protégées.

**Mots-clés** : Suivi des mammifères, Conservation, Pièges photographiques, Connaissances écologiques locales, Traits d'histoire de vie

# Abstract

## **Spatio-temporal use of multifunctional anthropogenic landscapes by African mammals. Testing the principle of anthropodependence.**

Global biodiversity is suffering a sixth mass extinction mainly due to human activities. It cannot be preserved by protecting only 30% of the Earth's surface, as foreseen in the COP15 targets. Researchers have suggested the establishment of 'shared Earth' between humans and wildlife to ensure connectivity between protected areas and to reconnect humans and nature. To do this, it is necessary to know what wild mammals can use human-modified habitats, how they do it, and which life history traits allow them to benefit from these new environments. Indeed, the conceptual model on anthropodependence predicts different uses of space and anthropogenic resources depending on the species. The spatio-temporal behavior of wild mammals in the Garden Route Biosphere Reserve, a multifunctional landscape in South Africa, was monitored using camera traps and an online questionnaire. Combining these methods provides additional information, increases spatial coverage and data, and involves various stakeholders in the conservation process. The use of the anthropogenic habitats and the tolerance of mammals to human disturbance (direct or structural) was found to be species-dependent, reflecting the diversity of strategies developed by the species. Temporal avoidance of humans, however, appears to be the most common strategy. Areas highly modified by human appeared to be more favorable to smaller species and species with generalist diets rather than strict carnivore. The preservation of natural habitats in anthropogenic habitats, for which private initiatives are fundamental, allows certain mammals to use anthropogenic habitats, which makes shared habitats an asset for the conservation of certain species, in support of protected areas.

**Keywords:** Mammal monitoring, Conservation, Camera traps, Local ecological knowledge, Life history traits