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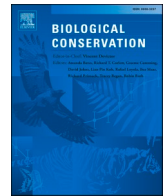
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# A local ecological knowledge-based assessment of anthropodependence for large mammals in anthropogenic landscapes

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## ABSTRACT

Humans have shaped the environment through landscape transformation, disturbance, and resource exploitation, leading to major habitat modification and fragmentation. Mammal species are massively threatened by these changes and their diversity implies various responses to human disturbance. It is essential to understand the conditions for their persistence in human-dominated landscapes, and the drivers of humans-mammals' coexistence to apply relevant conservation measures. The Garden Route Biosphere Reserve, in South Africa, a mosaic landscapes where human activities and wildlife meet, is an ideal site to examine how anthropogenic attributes influence wildlife occurrence. To maximise our area coverage through a replicable, low-cost protocol, we designed an online survey aimed at residents to investigate the effect of landscape metrics and property attributes — the availability and type of anthropogenic resources, the integrity and type of natural habitats, structural disturbances and interferences — on the persistence of mammals in such environments. We collected data from 247 respondents and modelled the drivers of occurrence for 14 mammal species (>500 g). We found species-specific responses to synthetic variables describing anthropogenic features in the studied landscape and used the anthropodependence framework to categorise species profiles. We showed that human disturbance combined with the availability of anthropogenic resources and natural habitats defined various categories of species profiles, which should require differential conservation actions. Local ecological knowledge proved promising to understand conditions for mammal persistence in human-dominated landscapes. This method also allowed researchers to engage with a wide variety of stakeholders, thus creating a hub for knowledge exchange.

## 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). Presently, 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 in conservation, aiming at preserving suitable habitats for biodiversity. However, their effectiveness is context-dependent and sometimes contested (Craigie et al., 2010; Gatiso et al., 2022; Geldmann et al., 2019). In order to increase the habitats suitable for wildlife, researchers have called for designing 'shared' spaces

between humans and wildlife to complement strictly protected areas (Obura et al., 2021; Rosenzweig, 2003). Indeed, preserving natural spaces within human-dominated landscapes is critical for the persistence of numerous vertebrates species (Downs et al., 2021). However, these areas could become the scene of tensions and conflicts between human activities and wildlife. Human-wildlife coexistence, defined by Carter and Linnell (2016) as a dynamic but sustainable state where both humans and wildlife co-adapt to living in shared landscapes, still constitutes a major challenge. To be successful, this co-adaptation requires animals to occupy landscapes shared with humans, and humans to tolerate the presence of wildlife in their vicinity (Carter and Linnell, 2016). Furthermore, such shared spaces also provide critical

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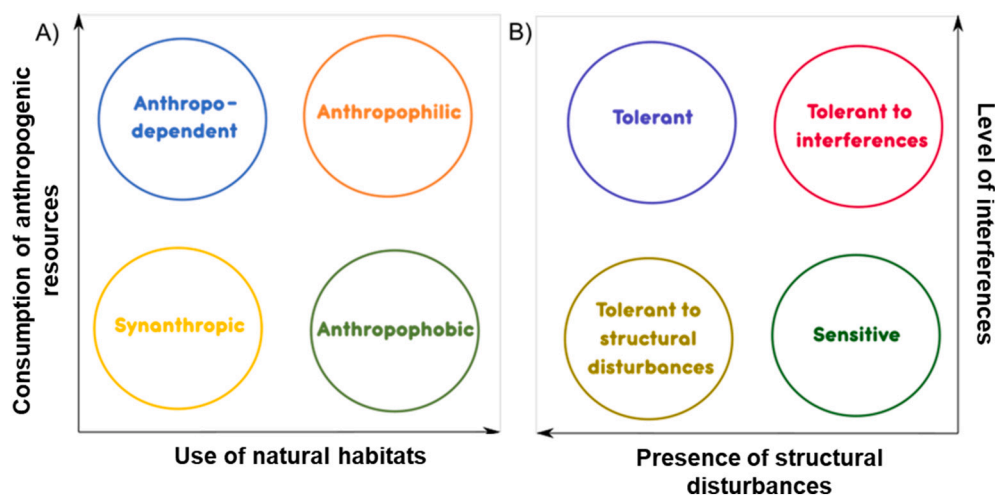
connectivity between protected areas as well as opportunities for humans to reconnect with nature (Obura et al., 2021).

Not all wild mammal species are expected to exhibit the same responses to anthropogenic disturbance and habitat modification. Some species may not persist in anthropogenic environments (Sebastián-González et al., 2019), while others may thrive because of novel predation opportunities or refugia (Fleming and Bateman, 2018). This could result in the modification of species community composition and trophic webs (Sévêque et al., 2020). These modified communities are often dominated by species that adapt their diet in anthropogenic environments in response to different resource availability (Drouilly et al., 2018; Leighton et al., 2022; Widdows and Downs, 2015). Predators, such as mammals (e.g. red foxes, *Vulpes vulpes* and caracal, *Caracal caracal*) or birds (e.g. house sparrows, *Passer domesticus*), are examples of such species benefiting from human landscape modification through predation on species commensal to humans, such as rodents or domestic animals (Fleming and Bateman, 2018; Natrass and O’Riain, 2020).

Hulme-Beaman et al. (2016) proposed a framework for classifying species response to human transformations based on their home-range overlap with anthropogenic environments and anthropogenic resource consumption. They separated them into four groups: anthropophilic, synanthropic, anthropophobic and commensal populations (Fig. 1A). The dependence on human resources by some wild animals often leads to an impact on humans, which makes the definition of commensal species unadapted in an anthropogenic context. Hulme-Beaman et al. (2016) qualify commensal populations which are associated with a dependence to anthropogenic resource as ‘anthropodependent’ populations. To the best of our knowledge, this framework has not been previously tested on a community of medium to large mammals. Further, modification of spatio-temporal niche partitioning is a common outcome of mammal adaptation to anthropogenic disturbances (Sévêque et al., 2020). In their review on the influence of human disturbance on the spatial, temporal and niche overlap between carnivore communities, Sévêque et al. (2020) grouped human disturbances into two categories: top-down disturbance, corresponding to direct human presence (e.g., recreational activities, hunting and pets), and bottom-up disturbance, corresponding to land modification (e.g., built-up environments and agricultural land uses; Fig. 1B). Both types of

disturbance often have consequences for wild mammal habitat use (Larson et al., 2016; Nickel et al., 2020). These effects can be additive or compensatory, leading to masked responses, which calls for considering these two forms of human disturbance separately when evaluating anthropogenic impacts on wildlife (Nickel et al., 2020; Sévêque et al., 2020). For instance, species can adapt to human-dominated habitats by shifting their core home-range to avoid human encountering (Van Scoyoc et al., 2023). Testing the combination of the Hulme-Beaman et al. (2016) and the Sévêque et al. (2020) frameworks and assessing the position of different species within it can be extremely useful in designing appropriate and effective conservation measures, tailored to the behaviour of species in a particular context. Further, better understanding species responses to anthropogenic contexts should help building a resilient coexistence between mammal species and humans in shared landscapes (Carter and Linnell, 2023).

Research on mammal responses to anthropogenic landscape transformation has mainly focused on data based on ecological approaches, such as camera trap surveys, movement or diet studies (Drouilly et al., 2018; Ngcobo et al., 2019; Nickel et al., 2020). Setting up fine-scale wildlife monitoring protocols can become a challenge in fragmented or mosaic landscapes because of the diversity of land tenure (private and public properties), land uses (natural, agricultural and urban environments) and the multiple interfaces. In such heterogeneous context, harnessing local ecological knowledge offers a valuable method for gathering information on wildlife occurrence, residents’ practices and tolerance, as well as monitoring conservation or environmental management measures (McKinley et al., 2017; Pédarros et al., 2020; Streicher et al., 2021; Widdows and Downs, 2017). While having demonstrated benefits, participatory research methods also have elicited concerns, just as any other methods (Camino et al., 2020; Devictor et al., 2010; McKinley et al., 2017). For instance, the accuracy of the data collected in terms of species identification, location and timing requires time investment to ensure adequate quality (Devictor et al., 2010; McKinley et al., 2017; Young et al., 2019). Although an increasing number of studies are using participatory approaches (Dickinson et al., 2012; McKinley et al., 2017; Swanson et al., 2015; Young et al., 2019), few have focused on collecting information on mammal species occurrence using local-ecological knowledge (Burt et al., 2021; Camino et al.,



**Fig. 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 represent top-down disturbances described in Sévêque et al. (2020), whereas structural disturbances refer to the bottom-up disturbances. Tolerant species (high interference and structural disturbance) might be anthropodependent species; species tolerant to humans but not infrastructure (high interference, low structural disturbance) are more likely to broadly be the profile of anthropophilic species; species tolerant to humans but not infrastructure (low interference, high structural disturbance) correspond 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.

2020; Dickinson et al., 2012; Pédarros et al., 2020; Zwerts et al., 2021). Questionnaire-based surveys have shown to be an interesting tool to study human-wildlife interactions, allowing for the collection of a large amount of data on wildlife presence, including behaviour, as well as on human practices and perceptions of their environment (Camino et al., 2020; Streicher et al., 2021; White et al., 2005; Widdows and Downs, 2017).

The aim of this study was to understand how the community of medium and large mammal species (>500 g) responded to heterogeneous and mosaic anthropogenic landscapes and what factors influenced individual species or a community of species presence, using data from residents' observations at property level. The study was conducted in the Garden Route Biosphere Reserve (GRBR), a mosaic of land uses that forms part of the Cape Floristic Region (Weinzettel et al., 2018), where protected areas interface with agricultural, residential and urban areas. Biosphere reserves are recent governance models that aim to combine socio-economic dimensions and biodiversity conservation in protected areas and their surroundings (Pool-Stanvliet and Coetzer, 2020). In the area, the studied mammal community is very diverse and have differences in weight (500 g to 52 kg), ecological requirements 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 the purpose of this study (Santini et al., 2019). We combined the conceptual frameworks proposed by Hulme-Beaman et al. (2016) and Sévêque et al. (2020), to characterise mammal communities and species persistence in this human-modified landscape as a function of habitats, resources, interferences and structural disturbances (Fig. 1).

## 2. Materials and methods

### 2.1. Study area

The GRBR is located on the south-eastern coast of South Africa, between the Indian Ocean and Outeniqua Mountains, and covers an area of approximately 700,000 ha (Fig. 2). 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). As of 2019, the population of the Garden Route District Municipality was 620,000 and the population is expected to keep growing (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 (GRNP), a non-fenced protected area managed by South African National Parks (SANParks) and covering 17 % (121,000 ha) of the GRBR, was established in 2009 with the primary objective of protecting remnant patches of indigenous forest. The GRBR is the ninth in South Africa to be recognised by UNESCO (Pool-Stanvliet and 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 parts of the landscape required to achieve ecosystem and species conservation objectives.

### 2.2. Study design

#### 2.2.1. Data collection

Based on preliminary discussions with local conservation organisations, an online 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 and perceptions. The first version of the questionnaire was submitted to local conservation organisation for comments and inputs. The questionnaire was then piloted face-to-face and online with 20 volunteers and subsequently revised following their recommendations. The final questionnaire consisted of nine parts and 59 questions, most of which were multiple-choice to avoid subjective interpretation (see questionnaire Appendix 1). The participation to this research was totally voluntary. The survey was administered through the platform SurveyMonkey to reach a broad audience (though limited to those having internet access). The survey targeted residents of the GRBR, with the aim to randomly sample a diversity of properties, participants, habitats and land uses. The questionnaire was sent using mailing lists obtained from CapeNature, SANParks, the Wildlife and Environment Society of South Africa and local conservancies. The link to the questionnaire survey was also published on multiple WhatsApp and Facebook groups in the different local municipalities as well as in local newspapers (*George Herald* and *The Edge*). The survey was accessible online from November 2021 to March 2022 and reminders were sent in December and February. The questionnaire was available in English and Afrikaans, as these are the two most spoken languages among landowners in the study area. To preserve their anonymity, participants were

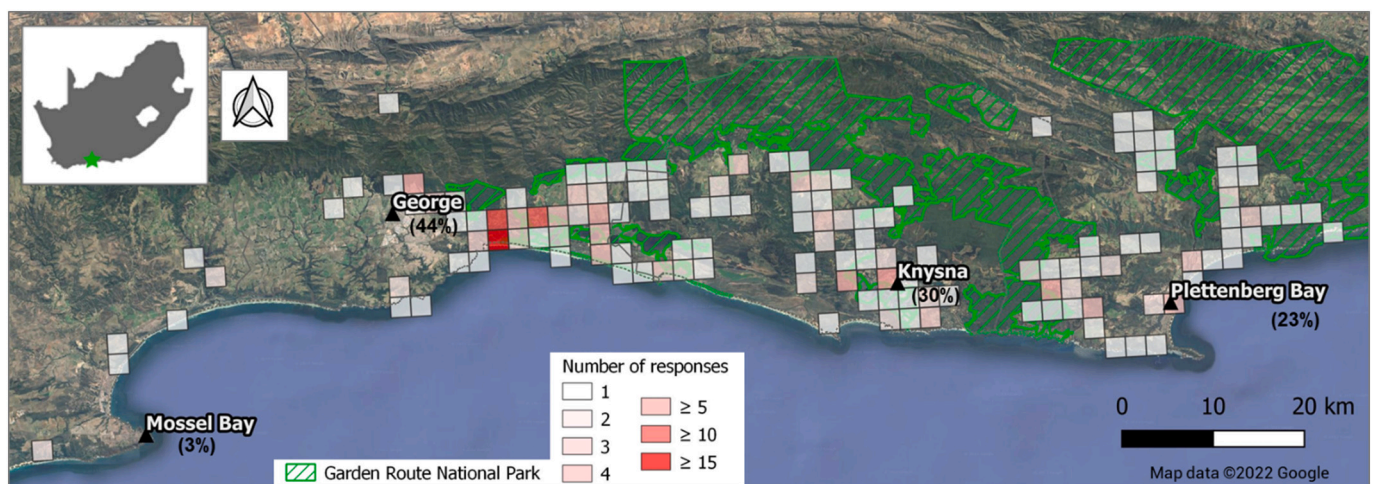


Fig. 2. Study site in the Garden Route (green star), South Africa. The cells represent the survey grid, and are coloured by the number of responses. The borders of the Garden Route National Park are represented in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



asked to indicate the general location of their property on a cell of 2.23 \* 2.23 km on a map. This research protocol was approved by the Nelson Mandela University Research Ethics Committee (H20-SCI-SRU-002), SANParks (BERN-A/2020-008) and CapeNature (CN44-87-16198) permits.

## 2.2.2. Data processing

**2.2.2.1. Property characterisation.** To describe the diversity of properties sampled, we built variables from 12 questions to produce gradients for each of the following dimensions of the conceptual model (Fig. 1): anthropogenic resources, natural habitats, structural disturbances and interferences. The questions and associated variables used are listed and described in Table S1.

First, to describe anthropogenic resources available on the respondents' properties, 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 <10 % variability (>90 % of either 1 or 0) were excluded from subsequent analyses. We also calculated a resource diversity index for each property by summing all the available resources, as we hypothesised that properties with higher resource diversity would attract more species (Hansen et al., 2020). 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). For each property, we considered a resource easily accessible when it was declared by respondents as previously used by wildlife on their properties. Second, because our default focus was on modified anthropogenic landscapes, we chose to describe the properties along a gradient of remaining natural habitats. We thus recorded the presence of natural habitats as well as their state (disturbed, under rehabilitation or natural) as self-reported by respondents, and assigned each 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, defined as bottom-up disturbances by Sévêque et al. (2020), 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 treated fences as a binary variable (taking 1 when present and 0 when absent), and the proportion of each property excluding wildlife as a numerical variable. We used these metrics as additional measures of infrastructural disturbance to describe the gradient of transformation from urban to agricultural landscapes in our study area. Fourth, to assess potential interferences, we were inspired by Sévêque et al. (2020). We used the binary variable of intentional killing (hunting, dog hunting, snaring and poaching), assigned a value of either 1 when present or 0 when 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). These variables represented the potential interferences encountered in the area.

We conducted multivariate analyses using the variables from the survey described above to build synthetic variables characterising the gradients along which the diversity of properties was distributed. We performed a principal component analysis when the analysis strictly included numerical variables (for the anthropogenic resource and natural habitat gradients; see Fig. S1) and a Hill and Smith analysis when numeric and categorical variables were combined (for the structural disturbance and interference gradients; see Fig. S2). The analyses were

conducted on R (R Core Team, 2020) using the 'dudi.pca' and 'dudi.hillsmith' functions of the 'ade4' package (Dray and Dufour, 2007).

**2.2.2.2. Species characterisation.** Species presence was assessed by a multiple-choice questions (e.g., 'At what frequency do the following species occur on your property?', not anymore, rarely, occasionally, frequently, very frequently). When we piloted the questionnaire, we realised that some respondents had challenges to identify mongooses and genets at species level, thus 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 each species 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. When a respondent did not answer the question for a given 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, frequently, occasionally or rarely, we assigned the variable a value of 1 (presence) (Table S1).

**2.2.2.3. Additional variables.** To assess the ecological knowledge of the respondents, we asked four questions. Two were based on identifying a species using a photograph: an herbivore (blue duiker, *Philantomba monticola*) and a mesocarnivore (Cape mongoose). The third required respondents to identify the track of a carnivore (caracal), and the fourth to identify the scat of an herbivore (porcupine, *Hystrix africaeustralis*). For each question, respondents were given three choices. To characterise the diversity of landscapes covered by the survey, we calculated the mean Human Modification Index (HMI) for each 2.23 \* 2.23 km cell, a value in the continuous range from 0 (no modification) to 1 (very high modification), (Kennedy et al., 2020). To estimate possible property geographical 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 also 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

We first tested the correlation between the eight synthetic variables describing property characteristics obtained from the four different multivariate analyses (Fig. 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 subsequent 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 models with a cumulative weight of <95 %. We averaged them (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, for each species, the sum of model weights per variable ('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 and Weisberg, 2019). All analyses were performed using R (R Core Team, 2020). We used the 'ggplot2' package for graphical representations (Wickham, 2016).

### 3. Results

We received a total of 262 individual questionnaire responses, of which 247 were complete. These included respondents from the four local municipalities (55 from Bitou, 110 from George, 72 from Knysna and eight from Mossel Bay; Table S4), who had lived in the GRBR for an average of 11.85 years (Fig. 2). The distribution of responses was relatively proportional to the population of the local municipalities except for Mossel Bay Municipality, which was under represented (WESGRO, 2021). 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 centroid of respondents' property cell and the closest boundary of the GRNP ranged between 0 and 52.3 km, with an average of 3 km.

#### 3.1. Species characterisation

One third of respondents obtained an ecological knowledge score above 75 %, and one third below 25 % (Fig. S4). 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 direct sightings (Table S2).















We obtained records for 25 different mammal species but given the relatively low ecological knowledge scores of some respondents, we only included the 14 most recorded species (Tables 2 and S5, Fig. S6). These 14 species were identified by >10 % of the respondents and consistently by respondents with high ecological knowledge. A camera trap survey done at the same period in the area was consistent with the species cited in the questionnaire (Bernard et al., 2024). An average of six different species were recorded per property (Fig. S5). Very common species included the bushbuck (80 % of the properties), porcupine (72 %) and vervet monkey (71 %). Rarer species (recorded on <25 % of properties) included the blue duiker, Cape grysbok, leopard, African clawless otter and common duiker (Table 1).

#### 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

**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>Galerella pulverulenta</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 %

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); the level of urbanisation gradient and level of connectivity; and different kinds of interferences, from dogs or humans (Table 2, Figs. S1, S2 and S7).

### 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 (Fig. S8, Table S4).

### 3.4. Species responses to anthropogenic variables

Species showed different responses to anthropogenic variables (Fig. 3). Diversity of natural habitats, urbanisation and availability of anthropogenic resources were the main synthetic variables determining the presence of mammal species on private properties in the GRBR (highest sum of model weight values per variable; Fig. 3, Table S5). They were followed by dogs, connectivity, hydromorphy, type of anthropogenic resource (farming vs. residential) and presence of humans. The predicted values, represented only for the three most important synthetic variables, showed different patterns between species (Fig. S9). Subsequent analyses and interpretations 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 to predict 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 associated with the availability and accessibility of anthropogenic resources (Fig. 3). 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 the accessibility of anthropogenic resources. The probabilities of otter and honey badger occurrence increased with increasing availability of anthropogenic resources. The probability of

occurrence of all omnivores also increased with increasing availability of anthropogenic resources. However, the probability of baboon and bushpig occurrence started lower than that of vervet monkeys, suggesting that baboons and bushpigs were more likely to be present on properties where anthropogenic resources were available (Fig. S9A). Blue duiker, common duiker and grysbok were negatively associated with farming activities ( $P < 0.05$ ; Fig. 3, Table S5) with the farming vs. residential gradient being the most significant variable to explain the probability of occurrence of the common duiker ( $P < 0.05$ ; Fig. 3, Table S5).

#### 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 (Fig. 3, Table S5). Genets, otters and mongooses (mesocarnivores) as well as the grysbok and common duiker (herbivores) were not significantly influenced by the diversity of natural habitats (Fig. S9B). Hydromorphy of natural habitats was not the most important synthetic variable for any species. However, caracal, porcupine and bushbuck significantly selected ( $P < 0.05$ ) for dryer habitats (Fig. 3, 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 (Figs. 3 and S9C, 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 (Fig. 9C). For only two herbivores — the grysbok and common duiker, the connectivity was significantly negatively correlated ( $P < 0.05$ ), with the probability of occurrence, implying that these species occur on properties with more fences, and particularly the common duiker (Fig. 3, Table S5).

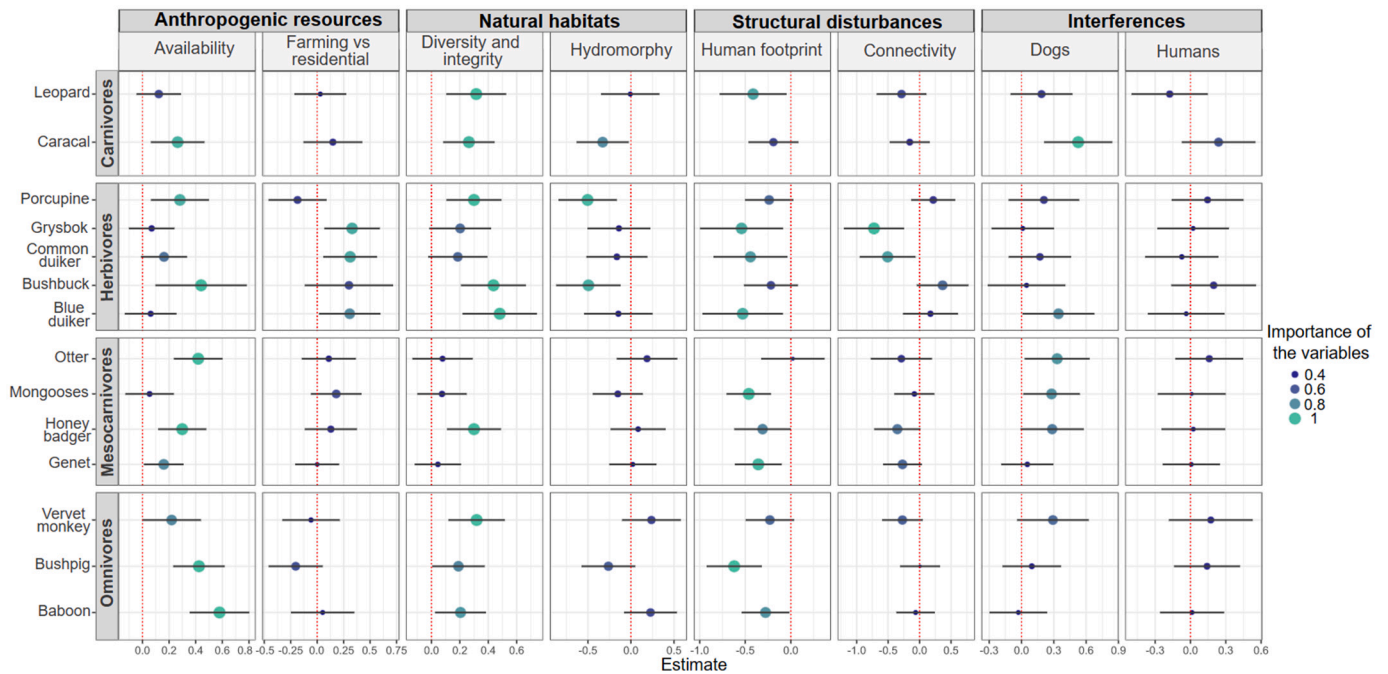
#### 3.4.4. Interferences

The caracal, blue duiker, otter, mongoose and honey badger were significantly positively associated with the presence of dogs (Fig. 3, Table S5). The presence of dogs was the most contributing variable in predicting the occurrence of caracals. None of the species significantly correlated with human interference (Fig. 3, Table S5).

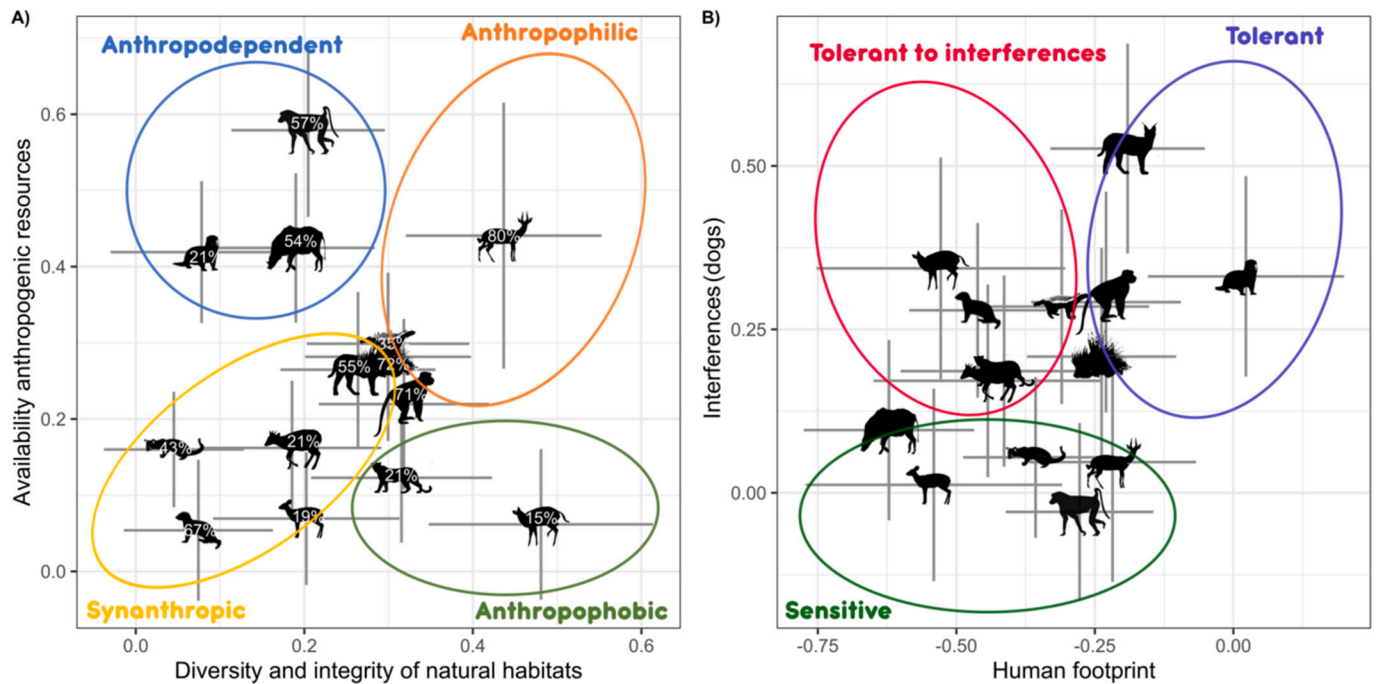
**Table 2**

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



**Fig. 3.** 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 model 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Estimates per species in relation to A) the diversity of natural habitats and availability of anthropogenic resources, B) the human footprint and the presence of dogs. Grey lines represent the standard error of each estimated value. Percentages indicate the proportion of properties where species were recorded. Coloured rings represent, for illustrative purposes, in A) 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; in B) the sensitivity of the species to interferences (presence of dogs) and structural disturbances (human footprint).



### 3.5. Testing the anthropodependence framework

We used the availability of anthropogenic resources and the diversity of natural habitats to produce a 2D representation of the anthropodependence framework proposed by Hulme-Beaman et al. (2016). Species displayed different responses to selected anthropogenic landscapes attributes (Fig. 4A). 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 were not strongly associated with the availability of 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 <20 % of properties. This low detection rate suggests that they have difficulties to persist in anthropogenic landscapes and could thus be classified as anthropophobic species. Interferences and human footprint affected species differently, and in turn certainly influence their position on the anthropodependence conceptual framework. Caracals, for instance, were tolerant to both types of disturbance, blue duikers and mongooses to interference only, whereas bushpigs and Cape grysboks were sensitive to human footprint only (Fig. 4B). No clear relationship was observed between human footprint and natural environments (Fig. S10A). Except for the bushpig, species attracted to properties where anthropogenic resources were available logically tended to be more tolerant to human footprint (Fig. S10B).

## 4. Discussion

Local ecological knowledge based on residents' observations enabled us to collect a large amount of information on the presence of mammals in human-modified landscapes. Our findings demonstrated that species had idiosyncratic responses to various anthropogenic factors, highlighting their various strategy to persist in anthropogenic landscapes. However, all species tended to be more present on properties with more natural habitats and with lower human footprint in their immediate neighbourhood, which provide important insights to explore new conservation pathways in shared landscapes. The diversity of species recorded by >10 % of respondents was consistent with previous studies and distribution maps (Endangered Wildlife Trust, 2020; Hanekom and Randall, 2015). The filtering of 10 % could be discussed as it may hide the detection of rarer species such as the lonely Knysna elephant (Moolman et al., 2019). However, rarely cited species could be the expression of species misidentification (e.g. the steenbok (*Raphicerus campestris*) or grey rhebok (*Pelea capreolus*) being confounded with the more widespread species such as the Cape grysbok or the bushbuck). Thus, the filtering provides a greater certainty that a species has been detected. Further, it was necessary to have a minimum sample size to robustly test for the apparent factors of mammals persistence in human-modified landscapes.

### 4.1. Using local ecological knowledge to monitor mammals in shared landscapes

The low contribution (low sum of model weight) of the interference variables (dogs and humans) in our models could result from the fact that we focused on human-dominated habitats (characterised by human presence), hence with little contrast along the gradient. This might have introduced a bias towards the detection of species not frightened by humans or dogs. Furthermore, it is possible that human presence itself have a lesser impact on the selection of habitats already disturbed compared to less disturbed habitats (Nickel et al., 2020), partly due to habituation. The positive values of the presence of dogs in the

occurrence model estimates probably highlight that people with dogs were more likely to detect species passing through their properties. Furthermore, 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. Further investigation should be conducted to properly test the effect of dog and human presence on the spatio-temporal niche of mammal species.

Most respondents were involved in conservation initiatives and thus despite our effort in enrolling participants from different angles (e.g. social-media, local newspapers; only 2 % were not part of a conservation project). We had no response from people living in informal settlement, which surely lead to bias on the perception and attitudes of the respondents that we measured. It is a minor issue for describing the presence of species, as we obtained a correct spatial description of the area with our current responses (informal settlement often represent a small spatial scale). Another limitation was associated with the necessity of having internet access to fill the survey, leading to another bias towards a portion of the possible respondents' population (Streicher et al., 2021), but the internet coverage in the GRBR is relatively high, limiting this source of bias. Considering our effort to reach all residents of the GRBR, in particular by using Facebook group of the different localities, this raises questions on the feasibility to include people from all horizon using only online survey and suggest the necessity of adding other protocol such as person-specific interview to target particular stakeholders and areas, or participatory mapping with focused groups (Pédarros et al., 2020).

Online questionnaires are open to various human biases, and inaccuracies may have been recorded because of respondents' difficulties with species identification (Anadón et al., 2010; Boakes et al., 2010; White et al., 2005). In addition, because humans are mainly active during the day, the sightings recorded in this survey might be biased towards diurnal and crepuscular species (Nyhus et al., 2003), or species that were more easily detected or identified (Pearce and Boyce, 2006). However, when comparing local knowledge with camera traps data we found no bias towards diurnal species but lesser detection of the smallest species (Bernard et al., 2024). Our study also highlighted a heterogeneous but rather low ecological knowledge among the residents, despite our bias towards residents involved in conservation programme and the relatively high occurrence of various mammals in anthropogenic landscapes. This stresses the need to improve environmental education in the GRBR. However, observed species ranged from charismatic to ordinary, small to large, and common to elusive, thus describing the diversity of species present in the GRBR. Because less charismatic (e.g. bushpig) and uncommon species (e.g. blue duiker) were reported frequently in this study, we can assume minimal bias associated with species status (Boakes et al., 2010). Furthermore, an increasing number of studies showed that local ecological knowledge can effectively describe the full suite of species in a mammal community (Bernard et al., 2024; Brittain et al., 2022; Burt et al., 2021; Zwerts et al., 2021); hence, our dataset obtained from over 200 observers likely describes the medium to large mammal community in the study area with a relative accuracy. 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 family trends. Even given these limitations local ecological knowledge can document the occurrence of wild mammals, particularly the most commonly observed species, in anthropogenic habitats and improve our understanding of ecological processes (Bernard et al., 2024). Overall, local ecological knowledge enables scientists to collect a large amount of data with limited time and cost, while providing with robust estimates, which is worth considering when requiring a quick assessment of the mammal community in an area.

In addition to its scientific benefits, local ecological knowledge-

based research promotes reconnection between people and their surrounding environment, including wildlife. In multifunctional landscapes such as those found in the GRBR, it could serve as the first step in designing resilient models for coexistence between humans, their activities and wildlife conservation (Devictor et al., 2010). Furthermore, as conservation measures need to be socially accepted to be effective, including a diversity of stakeholders into the conservation process is critical and will allow to develop trust towards scientists (Volski et al., 2021). Considering the trade-offs between biodiversity protection and poverty reduction in South Africa, involving people in co-constructed conservation projects can greatly benefit the development of sustainable conservation frameworks (Obura et al., 2021).

#### 4.2. Testing the anthropodependence conceptual framework

Local ecological knowledge enabled us to test the drivers of wildlife persistence and highlight the adaptation of mammals to human-dominated landscapes, which is critical to building human-wildlife coexistence scenarios (Carter and Linnell, 2023). The results based on the anthropodependence framework assumptions appeared consistent with those conceptualised by Hulme-Beaman et al. (2016), as illustrated by the diversity of response observed. Adding the response to human disturbances alongside resource availability and habitat attributes resulted in a finer description conceptualisation of species tolerance of, or sensitivity to, humans and their activities (Sévêque et al., 2020). The classification of baboons as anthropodependent was in agreement with other studies, based on their ability to adapt to and exploit anthropogenic environments (Hoffman and O’Riain, 2012; Mazue et al., 2023). Furthermore, the classification as anthropodependent is probably troop dependent as some troops still range mostly in protected areas, away from human habitats (Kennedy Overton et al., 2023). Although bushpigs find refugia in forests (Hanekom and 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 because of their sensitivity to high level of human footprint. These could also result from differences of behaviours in different populations as suggested by Hulme-Beaman et al. (2016). The bushbuck, caracal, honey badger, porcupine and vervet monkey seemed to exhibit anthropophilic or synanthropic profiles, which seems consistent 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 genets 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 genets and mongooses, these results may be inconclusive. 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, or rarely. 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. Because the blue duiker is a diet and habitat specialist, with highly specific ecological requirements, and sensitivity to human footprint, it is a good candidate for anthropophobic classification (Hanekom and Wilson, 1991; Venter et al., 2016). The common duiker, grysbok and leopard appeared to be anthropophobic species as well, which was consistent with their low observation rates. There could be variation of behaviour in leopard populations as they have been found to occur in farmland in other contexts (Athreya et al., 2016; Strampelli et al., 2018). 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. Further investigation is required to understand the ecology of this species in the GRBR. Overall, some species (e.g. bushbucks, baboons) exhibited a higher tolerance to human disturbances,

suggesting their higher capacity to persist in human-modified landscapes compared to others (e.g. blue duiker). We conclude that the disturbance dimension should be combined with the anthropodependence framework to better categorise species or populations, and advise on conservation actions.

#### 4.3. Implications for conservation and further research

All species exhibited a positive relationship with the presence and diversity of natural habitats, highlighting the major role that residents can play in encouraging wildlife persistence 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, especially anthropophobic species who may need to disperse between protected areas (Brennan et al., 2022; CapeNature, 2017). 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 (Downs et al., 2021; Obura et al., 2021). The South African National Biodiversity Infrastructure in their Biodiversity Spatial Planning recommends the implementation of Critical Biodiversity Areas in municipal Land-Use Planning. Given the critical role of natural habitat in anthropogenic landscape, we strongly encourage the legislated formalisation of such protection measure. This formalisation should be accompanied by an effort to educate residents living along these corridors to strengthen their participation in conservation efforts and promote a reconnection between people and wildlife in shared landscapes. These findings must be factored into the conception, design and implementation of conservation initiatives human-dominated landscapes. We highly recommend the development of a connectivity landscape, between land-sharing and land-sparing, in the mosaic landscape of GRBR as suggested by Grass et al. (2019), as found in similar multifunctional conservation landscapes, such as Trans-frontier Conservation Areas (Bourgeois et al., 2023). All species seemed to persist in the shared landscapes of the GRBR, but the coexistence between species and humans may differ, such as their conservation needs (Carter and Linnell, 2023). Our results suggest that conservation measures should be mindful of the requirement of each group described by Hulme-Beaman et al. (2016). Anthropophobic species occupy undisturbed natural habitats that can be found in protected areas. Therefore they strongly rely on conservation initiatives to persist in human-modified environments (Carter and Linnell, 2023). Synanthropic species would need corridors to move through the anthropogenic matrices, which could be the role played by Critical Biodiversity Areas (CapeNature, 2017). These species are likely to fit with a scenario of favourable coexistence with humans depending on the level of human adaptation (Carter and Linnell, 2023). As we did not explore the impact of recreational activities because we focused on private properties, it is possible that sensitivity to direct disturbance from recreation may modify species responses (e.g. Larson et al., 2016), in particular in landscapes promoting recreational activities such as the GRBR. Anthropophilic species persist in human-dominated landscapes as they take advantage of the presence of resources, however they can represent a sporadic nuisance for humans (Blanco et al., 2020; Carter and Linnell, 2023). It is therefore crucial to better understand how to increase human knowledge and tolerance towards wildlife and biodiversity in general, to encourage holistic land use planning to minimise tensions between conservation and other production systems and improve biodiversity monitoring in human-dominated landscape. This will only be achieved by promoting environmental education and implementing two-way communication channels between residents and conservation agencies, and by fostering practices and values that enable broader coexistence.

#### CRediT authorship contribution statement

**Alice Bernard:** Conceptualization, Data curation, Formal analysis,

Investigation, Methodology, Resources, Software, Visualization, Writing – original draft, Writing – review & editing. **Hervé Fritz:** Conceptualization, Funding acquisition, Project administration, Supervision, Validation, Writing – original draft, Writing – review & editing. **Anne-Béatrice Dufour:** Methodology, Software, Validation, Writing – review & editing. **Jan A. Venter:** Funding acquisition, Supervision. **Chloé Guerbois:** Conceptualization, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing.

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### Declaration of competing interest

The authors declare no conflict of interest.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110450>.

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