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Review

Bush Encroachment and Large Carnivore Predation Success in African Landscapes: A Review

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Abstract: Bush encroachment is a habitat change phenomenon that threatens savanna and grassland ecosystems worldwide. In Africa, large carnivores in bush encroached landscapes must adjust to increasing woody plant cover and biomass, which could affect predation success at multiple stages through complex and context-dependent pathways. We highlight, interpret, and compare studies that assessed how bush encroachment or related habitat parameters affect the predation stages of large African carnivores. Bush encroachment may directly or indirectly affect predation success in various ways, including by: (1) altering habitat structure, which may affect hunting efficiency and prey accessibility; (2) changing prey abundance/distribution, with smaller species and browsers being potentially favoured; (3) influencing interference competition within the carnivore guild. For habitat or dietary specialists, and subordinate predators that are vulnerable to both top-down and bottom-up ecosystem effects, these alterations may be detrimental and eventually incur population fitness costs. As the threat of bush encroachment continues, future studies are required to assess indirect effects on competitive interactions within the large African carnivore guild to ensure that conservation efforts are focused. Additionally, to better understand the effects of bush encroachment across Africa, further research is necessary in affected areas as overall little attention has been devoted to the topic.

Keywords: Africa; apex predator; bush cover; grassland ecology; habitat structure; predator–prey interactions; prey accessibility; prey availability; savanna ecology

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1. Introduction

Bush encroachment is defined as the increase in the density and biomass of woody plant species in grassland ecosystems [1,2]. Encroachment of woody vegetation occurs globally [1,3–6] and can lead to land degradation and possible habitat loss, habitat fragmentation and downstream ecosystem effects [1,7,8]. Evidence suggests that there are multiple interplaying causal factors, notably overgrazing by livestock, alterations in fire regimes, climate change and reduction or removal of browsing herbivores, including megaherbivores [9], which suppress woody biomass accumulation and regulate shrub density [10–13]. The issue is exacerbated in arid and semi-arid ecosystems that are prone to drought and high rainfall variability, such as much of the African continent [2,14]. Evidence is starting to emerge indicating that bush encroachment in African landscapes can alter the hunting habitats of large predators [2], for example by decreasing the availability of habitat edges used by large predators such as the cheetah (*Acinonyx jubatus*) to visualise and stalk prey [15,16]. Ecosystem effects of bush encroachment, such as increased bush density and altered prey availability, may influence the predation success of carnivores, but concrete evidence and synthesis are lacking. Furthermore, different hunting strategies

of competing predators and local contexts will likely lead to variable impacts of bush encroachment and altered levels of competition.

Animals may avoid predation in a number of ways, for example by avoiding predator-dense areas or by seeking refuge in safe patches in areas where perceived or actual predator densities are high [17]. Therefore, in addition to removing animals from the ecosystem via predation, predators influence prey densities and distributions by altering prey behaviour and forcing prey to employ avoidance mechanisms. Habitat features can provide refugia for small prey and decrease detectability, thereby facilitating predator avoidance [18,19]. In African savanna ecosystems, Guenther's dik-dik (*Madoqua guentheri*) is a small antelope species (ca. 5 kg) that prefers to forage in dense bushland habitats which are avoided by the larger-bodied impala (*Aepyceros melampus*; ca. 40 kg), which nonetheless overlaps substantially in diet with dik-dik [20]. The preference for dik-dik for bushland habitats has been attributed to a reliance on crypsis to avoid detection by predators [21]. In contrast, complex vegetation creates risky habitats for large prey such as Cape buffalo (*Syncerus caffer*), because large ambush predators such as lions (*Panthera leo*) can find concealment for ambush therein, and prey may struggle to escape due to vegetation barriers [22].

The effects of bush encroachment on carnivore predation success may be easier to predict when considering a simple food web, such as where only one carnivore is present, or where intraguild predation is absent or minimal [23]. In such systems, an absence or reduction in interspecific competition is likely to decrease pressure on predators that might otherwise be subordinate to larger carnivores; opening opportunities to locate safe optimal habitats for successful predation and consumption of prey. However, this is a rare scenario, as many ecosystems include diverse primary consumers and complex predator guilds [24]. Subordinate secondary consumers must hunt prey to survive while also avoiding predation and interference competition by dominant predators [25]. The effects of habitat change phenomena such as bush encroachment on competitive interactions within carnivore guilds are likely to be complex and highly context-dependent and have thus far been understudied.

To date, reviews on bush encroachment in ecology and conservation have focused on the causes of bush encroachment and effects on vegetation structure (e.g., [26–28]), with little attention paid to effects on predators. Previous discussion of effects on predators has been limited to general considerations supported by little evidence [29]. Our work herein complements previous outputs by highlighting, interpreting, and comparing studies that assess the effects of bush encroachment, or related habitat variables, on African predators and their prey in the context of predation success. Our focus is on large African carnivores (>15 kg). These species often exist in ecosystems heavily impacted by bush encroachment and are likely to be particularly affected by habitat change due to their large spatial requirements and high movement rates [30,31]. As predation success depends on multiple stages that may all be affected by bush encroachment, our review addresses bush encroachment effects on, and associations with, carnivore hunting behaviour at each stage of predation. Studies included mainly focus on predation on ungulate species, as these tend to be the preferred prey choice of large African carnivores [32–34]. The review concludes by discussing an important topic that has received little attention: competitive interactions among large carnivores in bush-encroached landscapes.

2. Methodology

2.1. Search Methodology for Publication Trends

To derive the number of outputs published annually for large carnivores from 2011 to 2020 (Figure 1), in March 2022 we conducted a search in Google Scholar using the combination of the words and phrases "bush encroachment", "Africa" and "large carnivore". We opted to use Google Scholar because it outputs more records than online publication databases such as Web of Science or Scopus [35,36]. By using Google Scholar, we increased

the chance that search outputs included reports, book chapters, and theses/dissertations, in addition to peer-reviewed scientific journal articles. This search engine was used exclusively in other recent reviews of topics in ecology and predator–prey interactions (e.g., [37–39]). To estimate the research effort on carnivores compared to herbivores, we performed an additional search replacing "large carnivore" with "large herbivore" and displayed the cumulative results on a clustered bar chart created in RStudio 2021.09.0 [40] (Figure 1).

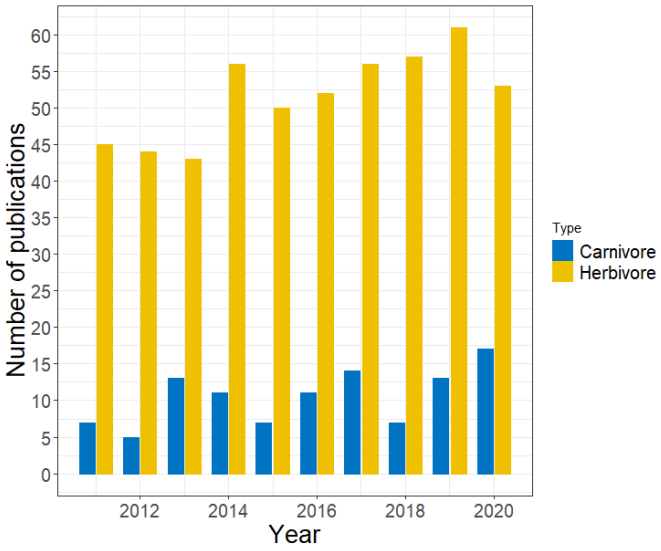

Figure 1. Annual frequency of publications relating to bush encroachment and large African carnivores for a recent 10-year period (2011–2020). Publications related to bush encroachment and herbivores are included for comparison. Search conducted in Google Scholar in March 2022.

2.2. Search Methodology for Comprehensive Review

To provide as comprehensive a search as possible for our review, we used the Clarivate Analytics Web of Science Core collection, the Elsevier Scopus database and Google Scholar to search for combinations of key words and terms periodically between May 2021 and July 2022. These three databases were used collectively in other ecological reviews of predator–prey relationships (e.g., [41–43]) and their combined use facilitates a broad overview of the target research topic. Specifically, Web of Science and Elsevier can produce search outputs that might be more specific to the search terms used, whereas Google Scholar supplements output by bringing in additional results from the peer-reviewed as well as grey literature [35,36]. Combinations of keywords and terms that we searched for (using the "Advanced document search" option in the Web of Science and the "All Fields" section in Scopus), included: "bush encroachment", "carnivore", "predator", "kleptoparasit*", "prey abundance", "prey accessibility", "Africa", "habitat", "habitat cover". These terms and words were also combined with the common names and scientific names for large African carnivore species.

To investigate the geographical distribution of relevant outputs that were returned from this search and used in the review synthesis and discussion (Table S1), we created a map in QGIS 3.10 [44] (Figure 2). A large proportion of the literature used in the synthesis and discussion (57%) pertained to the relationship between various vegetation or habitat factors and predation success without explicit reference to bush encroachment (Table S1). We included these on the map (marked with an asterisk) as we were able to use these outputs to make inferences about the possible effects of bush encroachment on predation success.

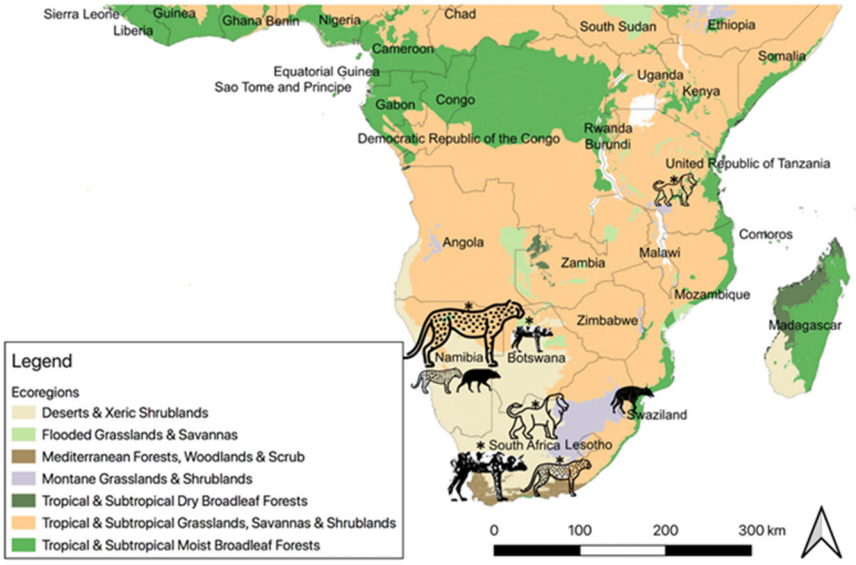

Figure 2. Distribution by country across Africa of publications relating to bush encroachment and large African carnivores that were identified in the review. Relative frequency of publications for each species indicated by size of icons; inclusion of paper(s) for species that assessed habitat variables without reference to bush encroachment indicated by an asterisk; cheetah, leopard, brown hyena, spotted hyena, lion, African wild dog. Data used to create map available in Table S1. Map generated in QGIS 3.10 (QGIS Association) [44]; map of Africa layer from ICPAC GeoPortal [45]; Ecoregion layer produced by Dinerstein et al. [46].

3. Current Knowledge

Large African carnivores and herbivores have not received the same amount of attention in the literature regarding bush encroachment (Figure 1). Annual search outputs returned from Google Scholar revealed a consistently and substantially lower volume of publications for carnivores than herbivores. A cyclic or potentially only slight increase in outputs over time is apparent for carnivores, whereas for herbivores the increase in outputs is more evident. There is therefore no evidence of rapid growth in research efforts for carnivores, even though bush encroachment is a critical conservation challenge in many grassland and savanna systems. This gap in research effort for carnivores is important to highlight and illustrates that overall, research assessing the effects of bush encroachment on predation success is rare. These effects can therefore mostly be inferred from research that has assessed associated habitat variables, such as vegetation density, vegetation cover and habitat visibility.

The search output for publications that we identified from the literature search, and used in the review discussion and synthesis, is visually summarised according to species and country in Figure 2. As this search returned no publications for African countries located outside of sub-Saharan Africa, the map extent in Figure 2 was limited to sub-Saharan Africa. As evidenced, study areas of published outputs are restricted mainly to southern Africa, particularly South Africa and Namibia with the largest focus being on the Namibian cheetah (*Acinonyx jubatus*) population.

The stages of predation are defined by Endler [47] as: search, encounter, kill and consumption. Each stage is influenced by multiple factors relating to habitat, predator and prey [48], which may all be affected directly or indirectly by bush encroachment [8,49]. For the purpose of this review, the additional stage "capture" will be referred to, as this takes place after an encounter, but may not lead to a kill.

3.1. Search, Encounter, Capture and Kill Stages

Because predators employ different hunting strategies, the success of predator search, encounter, capture and kill stages in bush-encroached areas likely varies between

species. The success of each stage may be determined by habitat structure, which could affect hunting efficiency and prey accessibility, and prey abundance and distribution, all of which may be influenced by bush encroachment [4,8,18].

3.1.1. Habitat Structure

Hunting Efficiency

Bush encroachment alters the predators' hunting grounds [50] (Figure 3a). Search and recognition may be diminished by the decreased sighting visibility that accompanies increased shrub cover, especially for predators that rely on the identification of prey from great distances [15,51]. Greater bush cover may decrease capture success for cursorial predators that are adapted to run by impeding prey chases while enhancing capture for ambush predators that can more easily conceal themselves to employ the sit-and-wait strategy [52,53]. Additionally, the dense bush may impede the movement of larger prey and displace these species [54]. Predators may then be required to hunt smaller prey more frequently to satisfy energy requirements, leading to increased hunting effort.

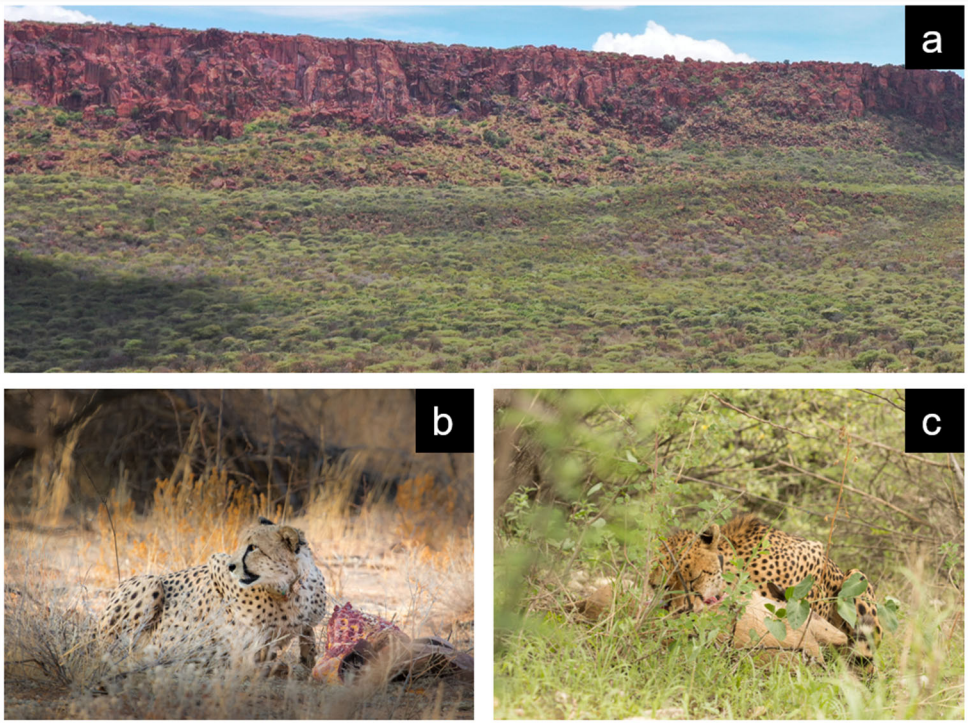

Figure 3. Bush encroachment affects various stages of predation, such as by impacting hunting efficiency and prey accessibility (**a**). Open areas are important for cursorial predators to detect and subdue prey and bush encroachment may affect capture success (**b**). Kleptoparasitism can decrease in bush-encroached areas, but in such areas, subordinate predators can be at greater risk of encountering dominant ambush predators (**c**). Photos by the Cheetah Conservation Fund.

Previous studies have indicated that male cheetah habitat selection is more strongly influenced by hunting requirements than prey density [55–59]. Muntifering et al. [18] and Nghikembua et al. [15] tracked cheetahs in north-central Namibia, where bush encroachment poses a threat to ecosystems [60] and identified significantly increased use of open shrubland and grassy areas, where sighting visibility was high. Habitat structure in open areas likely allows greater search and encounter success, as well as potentially providing the cheetah, a cursorial predator, with open areas to increase capture success (Figure 3b). Marker et al. [31] found that radio-tracked females in the same region preferred medium (30–75% canopy) bush areas and coalition males preferred thick bush habitats, but this habitat selection was not strongly correlated with the estimated presence of ungulate prey.

The purpose of their study was to determine large-scale cheetah habitat selection (home range) and therefore time intervals between relocations (4–7 days) were not small enough to determine fine-scale resource selection directly related to hunting. However, Bissett and Bernard [59] noted that hunting success was about the same (~50%) for cheetahs in both open and heavily wooded habitats in a South African reserve, where dense bush covered 70% of the area. Therefore, cheetahs are likely to be able to hunt efficiently in bush-encroached habitats, but the selection of these habitats to optimise hunting success is likely context dependent and may only be identified at the correct spatial scale.

Marker et al. [31] and Muntifering et al. [18] addressed a gap in the literature for long-term studies by using eight-year and seven-year datasets, respectively. Additionally, Marker et al. [31] analysed a large number of individuals/groups ($n = 41$). However, while these studies are representative of Namibian farmlands, many natural predators and competitors of the cheetah, such as lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) [17,61] have been extirpated from the region [50]. Findings from these studies therefore may not reflect cheetah habitat selection in ecosystems where intact large carnivore guilds are present.

Bush density was not found to be a significant determinant of cheetah habitat use by Muntifering et al. [18], who measured multiple habitat metrics and used these to develop a model through which cheetah high-use areas could be characterised. Other studies of carnivore habitat preference and abundance in bush-encroached areas measured additional vegetation variables, commonly shrub cover [62,63]. Failure of studies to detect a significant relationship between bush density and carnivore abundance or habitat preference could indicate that bush density may not always be the optimal variable to directly predict large carnivore habitat use in bush-encroached areas. Instead, bush density may indirectly affect habitat use, for example through effects on prey density or prey availability, or through decreasing grass cover that is relied on by some large predators [18,54]. In areas of moderate bush density, search, encounter and capture rates of prey may not be altered enough to change large carnivore abundances. Increased vegetative cover can also benefit predators, especially those using ambush strategies that rely on habitat cover to approach prey undetected; for example, lions have been shown to kill more frequently in densely vegetated areas [52,53]. Using Global Positioning System (GPS) collar data, Nghikembua et al. [15] found that cheetahs significantly avoided dense shrubland, where tree/bush density was greater than 75%. Cursorial predators such as the cheetah may avoid areas where bush density has surpassed a threshold and homogenised the landscape, as suitable hunting habitats are likely to be either lacking or non-existent.

Soto-Shoender et al. [63] found no significant effects of vegetation cover or season on spotted hyena abundance in two reserves of north-eastern Eswatini, presumably due to the very low detection rate of this species on camera traps. Studies that directly assess the effects of vegetation cover on the hunting success of large carnivores in Africa are lacking, and in the context of bush encroachment appear to be non-existent for most large carnivores. Therefore, it is difficult to determine the appropriateness of bush cover as a measure of bush encroachment impacts on large carnivore hunting efficiency. As detection rates of carnivores during ecological surveys can be low [63], future studies should fine-tune methods to enable higher detection rates and highlight any significant habitat associations.

A 2020 study surveying the response of predators in north-central Namibia to bush thinning [16] mitigated the low detection rates of some large carnivores by placing camera traps in areas of high detection, including scent-marking posts and trails [64–67], and by clearing areas around camera traps. The number of captures of leopards (*Panthera pardus*) and brown hyenas (*Parahyaena brunnea*) on camera traps was significantly higher in habitats where the bush was sparse, suggesting that habitat structure is important to these predators. This result was suggested to be due to higher ungulate abundance, as well as higher availability of habitat margins in less dense areas providing cover for stalking predators and increasing visibility of open areas where cursorial predators can easily

detect, chase and capture prey [2,15,18,68]. The latter conclusion is strengthened by findings from Nghikembua et al. [15], who observed that GPS-collared cheetahs frequently used habitat margins. Therefore, a homogenised landscape with no margins, for example, where bush encroachment is managed poorly or not at all, may provide poor hunting grounds for large predators by decreasing search, encounter and capture rates.

Although no studies appear to have assessed the effects of bush encroachment on African wild dogs (*Lycaon pictus*), landscape homogenisation may have similar effects on wild dog hunting success. Adaptation to landscapes homogenised by bush encroachment may be difficult for wild dogs, which tend to occupy areas with a mosaic of habitats [62,69]. Previous studies that have assessed wild dog habitat preference, show conflicting results, with more dense habitats being avoided in some cases [70] and preferred in others [69]. Whittington-Jones et al. [69] observed a strong preference for woodland habitats by wild dogs, despite low visibility in these habitats, and previous findings suggest that wild dogs prefer to hunt in woodland habitats [30,71]. However, prey capture success of wild dogs in relation to habitat type varies greatly within the literature [72–75].

The effects of bush encroachment on search, encounter and capture rates likely vary between large felids and canids due to reliance on different sensory systems to hunt. As felids rely primarily on vision to hunt [76], decreased visibility in dense habitats may greatly impair hunting success. However, the heightened sense of smell of canids, likely decreases reliance on high habitat visibility to detect prey and could lead to greater hunting success in bush-encroached habitats. For example, this is supported by findings from Krüger et al. [71], which suggested that lower visibility in denser habitats had little impact on prey capture success by wild dogs. Future research to compare the capture success of large felids and canids living in bush-encroached environments would be useful.

Prey Accessibility

Bush encroachment may influence capture success of prey by creating areas that alter prey accessibility. As accessibility is influenced by prey size, increased bush density may provide important refugia for smaller animals [19] but prevent escape of larger prey [54], making larger prey more accessible. Some predators, such as lions in the Serengeti [52], may prioritise prey accessibility over other factors such as prey abundance when choosing habitats for predation.

In Eswatini, Soto-Shoender et al. [63] observed increased species richness of mammals with increasing grass cover, which is negatively correlated with shrub biomass [4]. They also observed decreased ungulate species richness with increasing shrub cover and predicted a decrease in abundance of ungulate species with further bush encroachment. This supports findings from Smit and Prins [8] showing decreased species diversity and decreased densities of grazer species in Kruger National Park with increasing woody cover over a 7-year timeframe. Previous studies suggest that blue wildebeest (*Connochaetes taurinus*) avoid thickets due to higher predation risk, potentially to avoid stalking lions [77]. Findings from both Soto-Shoender et al. [63] and Smit and Prins [8] support this by revealing a significant decrease in wildebeest densities with increasing woody cover. Wildebeest density also significantly increased with increasing grass cover [63], which was partly attributed to the availability of quality forage. However, short grass enables predators to be spotted from greater distances and can allow quicker escapes [54], especially for larger prey that cannot take refuge in shrubs. Therefore, accessibility to larger prey such as wildebeest may be increased in bush-encroached areas.

Multiple studies have highlighted the influence of predation risk on habitat selection by prey species [78–81]. Smit and Prins [8] found a decrease in densities of four grazers, namely roan antelope (*Hippotragus equinus*), plains zebra (*Equus quagga*), sable antelope (*Hippotragus niger*) and eland (*Taurotragus oryx*), with increasing woody cover. This was attributed to the decreased forage availability that accompanied increased woody cover. However, Smit and Prins [8] did not assess predator-related factors, nor did they discuss the influence of predation risk, making it difficult to determine the effects of predators on

these prey densities. Furthermore, Soto-Shoender et al. [63] studied a fenced reserve where large predators consisted of low densities of spotted hyena and leopard, which may have resulted in prey utilising areas that elsewhere might have greater accessibility to predators. However, similar findings are described in other studies addressing predation risk; an association between numbers of larger herbivores and open areas, where visibility is higher, has been identified in Hluhluwe-iMfolozi Park, South Africa [81], where predators are abundant [82,83], and in Laikipia County, Kenya [84]. This further suggests that high grass cover—where bush encroachment is low [2]—leads to an increased chance of escape of large herbivores from large predators and therefore lower accessibility of prey.

Nghikembua et al. [16] assessed predator and prey presence in habitats of different post-bush thinning ages in Namibia. Differences relating to prey size were also assessed by analysing both large and small ungulate habitat preferences. They found no significant difference in camera-trap detection rates of ungulates or smaller, subordinate (meso) predators between thinned and non-thinned habitats, despite the finding that ungulate abundance was actually higher in thinned habitats. The authors suggested this to be the result of greater predator preference for thinned plots and the subsequent establishment of a "landscape of fear" [85], where ungulates and mesopredators feel unsafe in both thinned and non-thinned plots due to the high presence of large predators. Alternatively, this finding may have resulted from random variability in the data and small sample sizes or could indicate the importance of variability in habitat structure for prey when evading predation risk. Bush encroachment tends to increase habitat homogeneity and could therefore have an impact on predator–prey interactions by influencing the detection of prey, predator avoidance, and prey accessibility.

Shrub cover in savanna ecosystems can provide an important refuge for smaller animals [19,86] that may be predated by some large carnivores, such as rodent species and scrub hare (*Lepus saxatilis*) that have been identified in leopard scats [87,88]. Smit and Prins [8] found that average herbivore body size decreased with increasing woody cover. However, the prey size threshold at which bush cover becomes unsafe is unclear and, exceeding a bush density threshold may have negative consequences for those that have otherwise benefitted from the increased woody vegetation [15]. Smit and Prins [8] identified unchanged average herbivore biomass with increasing bush cover. However, the bush cover was only assessed up to 65%. Above this, herbivore biomass could decrease, and prey may consist primarily of smaller animals that may find refuge from large carnivores in densely vegetated areas.

3.1.2. Prey Abundance and Distribution

Prey availability can strongly influence carnivore demography [89]. Prey distribution and abundance are determined by the trade-off between food availability, competition and, as discussed, predation risk [48,90,91]. Increased competition and potential elimination of some herbivorous species may occur through decreased grazing capacity, as bush encroachment can decrease land productivity [2]. Multiple studies have discussed the effects of bush encroachment on herbivore abundance and distribution [63,92–94]. These parameters can affect predator search and encounter success, as fewer prey in an area may lead to increased search times and decreased encounters [48]. Low encounter rates with wild prey may then lead to higher levels of livestock predation [95].

Studies have predicted that bush encroachment in semi-arid ecosystems will lead to a shift in herbivore communities towards browsers [8,93,96] due to the replacement of grass with browse. Similar to Smit and Prins [8], Kiffner et al. [93] assessed changes in large herbivore densities in relation to bush encroachment. However, instead of assessing outcomes over a gradient of woody cover in a cross-sectional study, they assessed long-term population trends within a gradually changing landscape, allowing a better understanding of adaptive responses of wildlife populations. The study used a 58-year dataset of densities for 13 herbivore species in Lake Manyara National Park (LMNP), northern Tanzania, collected through total species counts (1959–2008) and line transect surveys

(2011–2016). Bush encroachment was determined by measuring habitat visibility in 2017 and comparing it with baseline data for 1985 and 1991 [97]. Access to such an extensive, long-term density dataset that can be tied to baseline vegetation data is lacking in the literature. Species counts collected prior to 2011 were argued to be reliable due to the small park size (~100 km^2) and the greater visibility afforded by a more open landscape during earlier years, an argument supported by the finding that horizontal visibility greatly reduced from 43–95% to 9–38% over the study period.

Reduced predator lines-of-sight, which are determined by measuring horizontal visibility, in LMNP were associated with increased bush encroachment, but Kiffner et al. [93] were unable to assess changes in other vegetation variables such as shrub height due to a lack of baseline data for these. However, predator sight lines are directly affected by bush encroachment [15,18,51], and this variable is therefore likely to be a good indicator of predator search and encounter success in bush-encroached landscapes. Reduced visibility was suggested by Kiffner et al. [93] to be partially responsible for the large decrease in density of waterbuck (a grazer; *Kobus ellipsiprymnus*) and sharp increases in densities of bushbuck (a browser; *Tragelaphus sylvaticus*) and impala (a mixed feeder; *Aepyceros melampus*). Similarly, Smit and Prins [8] found an increase in densities of two browsers, kudu (*Tragelaphus strepsiceros*) and giraffe (*Giraffa camelopardalis*), but a decrease in densities of most grazer species with higher woody cover. Interestingly, Kiffner et al. [93] also identified increased densities of wildebeest and zebra (both grazers). This finding partly aligns with predictions from Gordon and Prins [96] that, while ruminant bulk or roughage grazers (e.g., wildebeest) will decrease with increasing bush encroachment, grazers that are hind-gut fermenters (e.g., zebra) will increase, as they are less nitrogen-limited than ruminant bulk grazers. However, other factors unrelated to bush encroachment that were not measured in these studies will also influence herbivore densities, such as proximity to water sources [63] and land use pressures [98]. These findings should therefore be interpreted with caution.

If grazers are forced into bush-encroached habitats, they may experience higher predation risk than browsers due to reliance on long sight lines to detect predators, thereby enhancing predator capture success. A potential decrease in grazer numbers and a community shift towards browsers may have negative consequences for large predators that prey mainly on grazer species, such as lions [32]. However, lions may have an advantage over cheetahs as they are able to take down the largest browser species, including giraffes and young elephants (*Loxodonta africana*), which may be favoured in bush-encroached areas [8,93]. Leopards, lions and spotted hyenas also have a wider dietary niche breadth than cheetahs [99]. These species may be able to better adjust their diet to herbivore community shifts or reductions. Nonetheless, a meta-analysis by Khorozyan et al. [95] indicated that large ungulate availability significantly limits the survival of some large felids, including the lion, and that wild prey biomass most strongly predicts whether lions and leopards access alternative prey that incurs more risk. For example, these predators may resort to livestock predation and suffer persecution as a result. Kiffner et al. [93] showed that herbivore biomass decreases with increasing bush encroachment. In contrast, Smit and Prins [8] found that herbivore biomass remained the same with a greater bush cover but noted a reduction in prey size. Both effects could influence large predator hunting success, for example by increasing the abundances of smaller species that are harder to catch in areas with high refuge availability, or by reducing herbivore densities and decreasing encounter rates. Downstream effects of this may include increased livestock predation or increased competition between apex predators and the exclusion of subordinate predators such as cheetahs.

3.2. Consumption Stage

Consumption of prey by predators may be affected by the presence of kleptoparasites. Kleptoparasitism occurs when individuals from one species steal food procured by another species [100]. Because predator presence or abundance may be determined by the

extent of bush encroachment [16,18], kleptoparasitism rates may also be affected. Subordinate predators must select habitats that optimise both predation success and avoidance of apex predators that may kill them or steal their prey [61,101], with optimal sites sometimes occurring in dense vegetation [102]. Subordinate predators may establish a wide dietary niche to reduce competitive interactions with dominant predators or partition their resource use on fine temporal or spatial scales [103]. Some large subordinate predators, such as cheetahs, may hunt smaller prey that can be rapidly consumed to avoid detection by kleptoparasites [33]. This may lead to depleted energy intake with possible consequences for individual survival and overall population fitness.

Previous studies have focused on predator–prey relationships in relation to vegetation structure in African savannas and grasslands [104,105] and some have assessed competitive interactions between predators in these habitats [59,70,105,106]. However, studies on the latter topic are rare, especially in the context of habitat change resulting from bush encroachment.

The cheetah and the African wild dog are subordinate predators in the African large carnivore guild. Lion predation is the primary cause of cheetah mortality in the Serengeti [61] and a common cause of wild dog mortality in the Kruger National Park (KNP) [107]. Both the cheetah and the wild dog may also experience interference competition by lions and spotted hyenas via kleptoparasitism [68,108]. Despite this, and the vulnerable status of both species, no study has assessed the effect of bush encroachment on competitive interactions between these species and dominant predators. Mills and Gorman [70] observed significantly strong avoidance of *Acacia* thickets by wild dogs in KNP, despite the preference for this habitat type by impala, the preferred and most important prey species of wild dogs in this area. Playback experiments aiming to attract nearby competing carnivores such as lions to various habitats showed the common occurrence of lions in the three habitats most strongly avoided by wild dogs. This included two habitats where vegetation/bush density was high. It could therefore be inferred that, for wild dogs that are habitat generalists [30,109], the effects of bush encroachment on prey consumption may be indirect through the creation of more densely vegetated areas that support higher densities of lions and increase the risk of kleptoparasitism. However, the method used to measure habitat vegetation densities by Mills and Gorman [70] is not entirely clear and habitats were only broadly defined. Fine-scale habitat use in bush encroached areas, for example, the use of optimal patches to safely consume prey within areas of highly competitive pressure, requires further attention.

Gigliotti et al. [106] assessed cheetah survival in the context of predation risk, prey densities and habitat complexity in a reserve in northern KwaZulu-Natal, South Africa, and briefly discussed bush encroachment. Complex vegetation (dense habitat with high Enhanced Vegetation Index) was found not to be favoured by cheetahs, possibly because cheetahs are not protected from ambush predators here [110,111]. This aligns with findings from studies previously discussed suggesting that increased perceived predation risk is associated with shrub cover for larger prey animals [8,63,112]. Findings from the study are strong, as the authors assessed both seasonal (short-term) and long-term effects, monitoring the reserve monthly over a 10-year period and following a large number (n = 133) of individual cheetahs over their lifetime. However, one weakness of the study was the assessment of only one closed population. The same weakness can be identified in another study that assessed kleptoparasitism and predation of cheetahs in a fenced game reserve in South Africa [59]; the study found that kleptoparasitism increased in areas of lower cover and solitary females, which used thicket vegetation the most, experienced no kleptoparasitism when tracked continuously for 14 days, contradicting the suggestion by Gigliotti et al. [106] that cheetahs are less safe in thicket vegetation (Figure 3c). However, levels of kleptoparasitism were low overall, potentially because only one lion pride was present in the reserve and individual tracking periods were short.

In addition to subordinate predators, top predators within the African carnivore guild may also experience kleptoparasitism. In one study, lions succeeded in stealing

hyena kills with every attempt, even when outnumbered six to one [113]. Leopards in some populations frequently store and consume prey in trees [114,115], a unique strategy believed to be employed to avoid kleptoparasitism. A study in a South African reserve identified a 21% steal rate of leopard prey, with the primary kleptoparasite being the spotted hyena [115]. Brown hyenas are unique in the large African carnivore guild as in many regions they are primarily scavengers. Their presence may therefore be determined by the availability of carrion such as facilitated by the presence of other large carnivores, which provide potentially larger prey items to scavenge [116]. However, previous research has shown avoidance of competing top predators, such as the spotted hyena, by brown hyenas [117,118]. Studies regarding the scavenging success of brown hyenas in relation to vegetation cover are lacking, and with respect to bush encroachment are non-existent, making further discussion on this species difficult.

Lions are capable of stealing kills from Africa's top predators, including spotted hyenas [113] and leopards [115]. Loarie et al. [104] assessed the effect of vegetation structure on lion predation in KNP using Light Detection and Ranging (LiDAR) and GPS-tracking of lions. The study did not discuss bush encroachment despite this currently being a challenge faced in the park [119] but did find that male lions rested in more open areas than females, possibly to intimidate competitors. This reasoning is also given by Hopcraft et al. [52], who found a significant and positive association between scavenged kills and proximity to kopjes (rocky outcrops) used by plains lions, suggesting that lions used kopjes to identify scavenging, and presumably hunting opportunities. Bush cover may help predators decrease the chance of kleptoparasitism while consuming prey. However, Loarie et al. [104] found that male lions used areas of dense bush cover when hunting, where lines of sight were significantly lower. This was attributed to the ambush strategy favoured by male lions, compared with more cooperative hunting observed in female lion groups [120]. A balance between adequate cover and open habitat is likely required to allow fine-scale resource partitioning by predators in areas with complex and/or abundant carnivore guilds, and such a trade-off is probably unlikely to be obtained in homogenous highly bush-encroached areas, which also have lower prey biomass available. As a result, bush encroachment may lead to consistently low satiation levels in some large predator populations, which could affect population densities, fitness and survival.

4. Management Implications

Conservation efforts should aim to maintain intact carnivore guilds or restore guilds that have been simplified, for example as a result of human persecution. These guilds are key to ensuring healthy, balanced ecosystems, as they control prey abundance and diversity, suppress mesopredators that otherwise may alter ecological communities [121], and may also protect ecosystems from the effects of invasive species [122]. Management of bush-encroached habitats, for example through bush-thinning methods [123], should aim to optimise habitat utilization and promote predation success of endangered large carnivores, while also ensuring that patches of preferred habitat are available for prey species. Through the latter, a large wild prey base can be established, decreasing interference competition between carnivores and potential reliance on livestock depredation by large carnivores and subsequent human–carnivore conflict.

Various techniques may be used to identify thresholds at which to manage habitats for increasing or optimising predation success. Studies have often employed ground-based survey methods, measuring variables such as shrub density [18] and shrub cover [49,63] in sampling grids placed non-randomly or over vegetation gradients within habitats. These techniques may be more accessible and accurate within selected plots and may be the best options when identifying thresholds at which to manage habitats at a finer scale, for example, to preserve beneficial patches or habitat margins within larger landscapes. However, as some carnivores may select habitats at a broader (home range) scale to avoid encounters with top predators [124], it is important to utilise methods that allow

for feasible and time-efficient habitat assessment to inform management at the appropriate scale.

The availability of high-resolution remote sensing data has allowed for a fast, quantitative assessment of habitat variables that are indicative of bush encroachment over large areas. For example, woody vegetation cover, inclusive of both trees and shrubs, may be mapped for entire regions at high resolutions using synthetic aperture radar (SAR)-derived satellite data and remote sensing training data [125]. Using data produced via these methods, Atkinson et al. [126] determined fractional woody cover (FWC) thresholds conducive to high predation success for cheetahs and leopards in north-central Namibia. Optimal predation success was indicated to differ between carnivore species, suggesting that management of woody cover at certain thresholds may have species-specific benefits in this region. With the increasing availability of high-resolution remote sensing datasets, there is a greater opportunity to assess habitat thresholds at broader scales across Africa, which could allow for the development of standardised habitat management protocols.

In conjunction with habitat management, closed or fenced systems could benefit from close monitoring of predator and prey abundances and, if necessary, supplementation of these populations via translocation. This would help to minimise interference competition and the potential mortality of less dominant predators [124].

5. Conclusions and Future Research

Bush encroachment poses a challenge in savannas and grasslands throughout Africa and therefore requires further attention and research focus. Effects appear to be species and region-specific, but trends suggest a community shift towards browsing herbivorous species and smaller prey in bush-encroached areas, lower prey species diversity, as well as changes in prey availability, and possibly in vulnerability to predation. This may require some large carnivores to alter their hunting strategy or target less desirable prey, which may be easier to achieve for habitat and dietary generalists. Generally, it appears that areas with moderate bush and grass cover may be optimal for large predators, including the cursorial cheetah that may frequently use habitat margins to increase hunting success. However, above a certain threshold, bush encroachment may be detrimental to most predator and prey species, but this requires further investigation.

So far, most studies have been cross-sectional, providing good baseline data for future studies but failing to highlight adaptive responses of populations to bush encroachment over time as longitudinal studies would. Additionally, most studies, including longitudinal studies, have only assessed effects in small areas, which may be fenced reserves without emigration or immigration or areas where some large apex predators have been extirpated. Therefore, long-term as well as large-scale studies of populations that experience immigration and emigration and high kleptoparasitic pressure are needed to understand the effects of habitat change on the hunting success of large, vulnerable African carnivores. This understanding will be furthered with greater knowledge of prey habitat use in bush-encroached landscapes, which could be obtained if studies assess all three of the main prey habitat determinants: resource availability, predation risk and competition.

Understanding the drivers of bush encroachment and quantifying their relative as well as cumulative contributions, remain important focus areas for research. Efforts should continue to also focus on impacts on vegetation structure, composition and density triggered by altered herbivore communities, such as reduction or extirpation of megaherbivores, shifts in smaller herbivores from grazers to browsers, as well as overgrazing by livestock. The impacts of changes in fire regimes and the influence of climatic factors also need to be understood, as they will likely increasingly affect the ecology of African savannas and grasslands in complex and dynamic ways.

Ecological parameters of predator and prey populations, such as abundance and distribution, have received the most focus in the literature and, bush encroachment effects on predator populations as well as fitness effects have yet to be comprehensively assessed. Additionally, behavioural studies, particularly those assessing competitive interactions

among large carnivores in bush-encroached areas, are severely lacking and would likely yield context-dependent insights, suggesting that studies should occur across ecosystems and in varying carnivore guilds. For example, cheetahs and African wild dogs are threatened and endangered subordinate predators among large African carnivores, making them vulnerable to both top-down and bottom-up effects caused by bush encroachment; whereas in systems where lions and spotted hyenas have been lost, subordinate carnivores might have different responses in habitat selection with bush encroachment, due to absence of top-down regulation that operates in intact large carnivore guilds. High levels of kleptoparasitism, changes in hunting grounds and decreased prey abundance or diversity that may result from bush encroachment could decrease predation and handling success, increase levels of human–wildlife conflict, and further threaten these species. Future work should explore the indirect effects of bush encroachment on competitive interactions among large predators according to their hunting strategy, socio-biology, and dominance hierarchy, to inform the conservation of carnivores at most risk.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Publications assessing bush encroachment or related habitat variables in relation to large African carnivore species.

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References

1. Van Auken, O.W. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* **2000**, *31*, 197–215.
2. De Klerk, J.N. *Bush encroachment in Namibia. Report on Phase 1 of the Bush Encroachment, Monitoring and Management Project*; Ministry of Environment and Tourism: Windhoek, Namibia, 2004.
3. Jeltsch, F.; Milton, S.J.; Dean, W.R.J.; Van Rooyen, N. Analysing shrub encroachment in the southern Kalahari: A grid-based modelling approach. *J. Appl. Ecol.* **1997**, *34*, 1497–1508.
4. Hobbs, R.J.; Mooney, H.A. Community changes following shrub invasion of grassland. *Oecologia* **1986**, *70*, 508–513.
5. Singh, J.S.; Joshi, M.C. Ecology of the semi-arid regions of India with emphasis on land-use. *Dev. Agric. Manag. For. Ecol.* **1979**, *7*, 243–275.
6. Maestre, F.T.; Bowker, M.A.; Puche, M.D.; Belén Hinojosa, M.; Martínez, I.; García-Palacios, P.; Castillo, A.P.; Soliveres, S.; Luzuriaga, A.L.; Sánchez, A.M.; et al. Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecol. Lett.* **2009**, *12*, 930–941.
7. Angassa, A. Effects of grazing intensity and bush encroachment on herbaceous species and rangeland condition in southern Ethiopia. *Land Degrad. Dev.* **2014**, *25*, 438–451.
8. Smit, I.P.; Prins, H.H. Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. *PLoS ONE* **2015**, *10*, e0137857.
9. Bakker, E.S.; Gill, J.L.; Johnson, C.N.; Vera, F.W.; Sandom, C.J.; Asner, G.P.; Svenning, J.C. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 847–855.
10. Bond, W.J.; Midgley, G.F. A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas. *Glob. Chang. Biol.* **2000**, *6*, 865–869.

11. Augustine, D.J.; Mcnaughton, S.J. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* **2004**, *41*, 45–58.
12. Coetzee, B.W.; Tincani, L.; Wodu, Z.; Mwasi, S.M. Overgrazing and bush encroachment by *Tarchonanthus camphoratus* in a semi-arid savanna. *Afr. J. Ecol.* **2008**, *46*, 449–451. https://doi.org/10.1111/j.1365-2028.2007.00842.x.
13. Scheiter, S.; Higgins, S.I. Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Glob. Chang. Biol.* **2009**, *15*, 2224–2246.
14. Groengroeft, A.; de Blécourt, M.; Classen, N.; Landschreiber, L.; Eschenbach, A. Acacia trees modify soil water dynamics and the potential groundwater recharge in savanna ecosystems. In *Climate Change and Adaptive Land Management in Southern Africa-Assessments, Changes, Challenges, and Solutions*; Revermann, R., Krewenka, K.M., Schmiedel, U., Olwoch, J.M., Helmschrot, J., Jürgens, N., Eds.; Klaus Hess Publishers: Göttingen, Germany; Windhoek, Namibia, 2018; pp. 177–186.
15. Nghikembua, M.; Harris, J.; Tregenza, T.; Marker, L. Spatial and temporal habitat use by GPS collared male cheetahs in modified bushland habitat. *Open J. For.* **2016**, *6*, 269–280.
16. Nghikembua, M.T.; Marker, L.L.; Brewer, B.; Mehtätalo, L.; Appiah, M.; Pappinen, A. Response of wildlife to bush thinning on the north central freehold farmlands of Namibia. *For. Ecol. Manag.* **2020**, *473*, 118330.
17. Durant, S.M. Competition refuges and coexistence: An example from Serengeti carnivores. *J. Anim. Ecol.* **1998**, *67*, 370–386.
18. Muntifering, J.R.; Dickman, A.J.; Perlow, L.M.; Hruska, T.; Ryan, P.G.; Marker, L.L.; Jeo, R.M.; Managing the matrix for large carnivores: A novel approach and perspective from cheetah (*Acinonyx jubatus*) habitat suitability modelling. *Anim. Conserv.* **2006**, *9*, 103–112.
19. Loggins, A.A.; Shrader, A.M.; Monadjem, A.; McCleery, R.A. Shrub cover homogenizes small mammals' activity and perceived predation risk. *Sci. Rep.* **2019**, *9*, 1–11.
20. Otieno, T.O.; Goheen, J.R.; Webala, P.W.; Mwangi, A.; Osuga, I.M.; Ford, A.T. Human- and risk-mediated browsing pressure by sympatric antelope in an African savanna. *Biol. Conserv.* **2019**, *232*, 59–65.
21. Brashares, J.S.; Garland, T.; Arcese, P. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behav. Ecol.* **2000**, *11*, 452–463.
22. Tambling, C.J.; Druce, D.J.; Hayward, M.W.; Castley, J.G.; Adendorff, J.; Kerley, G.I. Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology* **2012**, *93*, 1297–1304.
23. Melian, C.J.; Bascompte, J. Food web structure and habitat loss. *Ecol. Lett.* **2002**, *5*, 37–46.
24. Sih, A.; Englund, G.; Wooster, D. Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.* **1998**, *13*, 350–355.
25. Björklund, H.; Santangeli, A.; Blanchet, F.G.; Huitu, O.; Lehtoranta, H.; Lindén, H.; Valkama, J.; Laaksonen, T. Intraguild predation and competition impacts on a subordinate predator. *Oecologia* **2016**, *181*, 257–269.
26. Ward, D. Do we understand the causes of bush encroachment in African savannas? *Afr. J. Range Forage Sci.* **2005**, *22*, 101–105.
27. O'Connor, T.G.; Puttick, J.R.; Hoffman, M.T. Bush encroachment in southern Africa: Changes and causes. *Afr. J. Range Forage Sci.* **2014**, *31*, 67–88.
28. Belayneh, A.; Tessema, Z.K. Mechanisms of bush encroachment and its inter-connection with rangeland degradation in semi-arid African ecosystems: A review. *J. Arid Land* **2017**, *9*, 299–312.
29. Joubert, D.F.; Zimmermann, I. The impacts of wood harvesting of bush thickening species on biodiversity and ecological processes. In Proceedings of the First National Forestry Research Workshop, Windhoek, Namibia, 12–13 March 2002; Forestry Publication, Ministry of Environment and Tourism: Windhoek, Namibia, 2002; Volume 9, pp. 67–78.
30. Andreka, G.; Linn, I.J.; Perrin, M.R.; Maddock, A.H. Range use by the wild dog in Hluhluwe Umfolozi Park, South Africa. *South Afr. J. Wildl. Res.* **1999**, *29*, 1–9.
31. Marker, L.L.; Dickman, A.J.; Mills, M.G.; Jeo, R.M.; Macdonald, D.W. Spatial ecology of cheetahs on north-central Namibian farmlands. *J. Zool.* **2008**, *274*, 226–238.
32. Hayward, M.W.; Kerley, G.I. Prey preferences of the lion (*Panthera leo*). *J. Zool.* **2005**, *267*, 309–322.
33. Hayward, M.W.; Hofmeyr, M.; O'Brien, J.; Kerley, G.I. Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): Morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *J. Zool.* **2006**, *270*, 615–627.
34. Hayward, M.W.; Henschel, P.; O'Brien, J.; Hofmeyr, M.; Balme, G.; Kerley, G.I. Prey preferences of the leopard (*Panthera pardus*). *J. Zool.* **2006**, *270*, 298–313.
35. Harzing, A.-W.; Alakangas, S. Google Scholar, Scopus and the Web of Science: A longitudinal and cross-disciplinary comparison. *Scientometrics* **2016**, *106*, 787–804.
36. Martín-Martín, A.; Orduna-Malea, E.; Thelwall, M.; López-Cózar, E.D. Google Scholar, Web of Science, and Scopus: A systematic comparison of citations in 252 subject categories. *J. Informetr.* **2018**, *12*, 1160–1177.
37. Hirt, M.R.; Tucker, M.; Müller, T.; Rosenbaum, B.; Brose, U. Rethinking trophic niches: Speed and body mass colimit prey space of mammalian predators. *Ecol. Evol.* **2020**, *10*, 7094–7105.
38. Chitwood, M.C.; Baruzzi, C.; Lashley, M.A. "Ecology of fear" in ungulates: Opportunities for improving conservation. *Ecol. Evol.* **2022**, *12*, e8657.
39. Cristescu, B.; Elbroch, L.M.; Dellinger, J.A.; Binder, W.; Wilmers, C.C.; Wittmer, H.U. Kill rates and associated ecological factors for an apex predator. *Mamm. Biol.* **2022**, *102*, 291–305.
40. RStudio Team. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. 2021. Available online: https://www.rstudio.com/products/rstudio/older-versions/ (accessed on 10 July 2022).

41. Luna, Á.; Romero-Vidal, P.; Arrondo, E. Predation and scavenging in the city: A review of spatio-temporal trends in research. *Diversity* **2021**, *13*, 46.
42. Wirsing, A.J.; Newsome, T.M. Scavenging effects of large Canids. *Integr. Comp. Biol.* **2021**, *61*, 117–131.
43. Karandikar, H.; Serota, M.W.; Sherman, W.C.; Green, J.R.; Verta, G.; Kremen, C.; Middleton, A.D. Dietary patterns of a versatile large carnivore, the puma (*Puma concolor*). *Ecol. Evol.* **2022**, *12*, e9002.
44. QGIS Development Team. QGIS Geographic Information System. QGIS Association. Open Source Geospatial Foundation Project. 2020. Available online: http://qgis.osgeo.org (accessed on 3 July 2022).
45. ICPAC GeoPortal. Africa Shapefiles. openAFRICA. Available online: https://open.africa/dataset/africa-shapefiles (accessed on 3 July 2022).
46. Dinerstein, E.; Olson, D.; Joshi, A.; Vynne, C.; Burgess, N.D.; Wikramanayake, E.; Saleem, M. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* **2017**, *67*, 534–545.
47. Endler, J.A. Defense against predators. In *Predator-Prey Relationships: Perspective and Approaches from the Study of Lower Vertebrates*; Federand, M.E., Lauder, G.V., Eds.; University of Chicago Press: Chicago, IL, USA, 1986; pp. 109–134.
48. Gorini, L.; Linnell, J.D.; May, R.; Panzacchi, M.; Boitani, L.; Odden, M.; Nilsen, E.B. Habitat heterogeneity and mammalian predator–prey interactions. *Mammal Rev.* **2012**, *42*, 55–77.
49. Blaum, N.; Rossmanith, E.; Popp, A.; Jeltsch, F. Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecologica* **2007**, *31*, 86–92.
50. Marker-Kraus, L.; Kraus, D.; Barnett, D.; Hurlbut, S. *Cheetah Survival on Namibian Farmlands*, 3rd ed.; Solitaire Press: Windhoek, Namibia, 2003.
51. Arbieu, U.; Grünewald, C.; Schleuning, M.; Böhning-Gaese, K. The importance of vegetation density for tourists' wildlife viewing experience and satisfaction in African savannah ecosystems. *PLoS ONE* **2017**, *12*, e0185793.
52. Hopcraft, J.G.C.; Sinclair, A.R.E.; Packer, C. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.* **2005**, *74*, 559–566.
53. Davies, A.B.; Tambling, C.J.; Kerley, G.I.; Asner, G.P. Effects of vegetation structure on the location of lion kill sites in African thicket. *PLoS ONE* **2016**, *11*, e0149098.
54. Martin, J.; Owen-Smith, N. Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Anim. Behav.* **2016**, *116*, 163–170.
55. Hunter, L.T.B. The Behavioural Ecology of Reintroduced Lions and Cheetah in the Phinda Resource Reserve, Kwazulu-Natal, South Africa. Ph.D. Thesis, University of Pretoria, Pretoria, South Africa, 1998.
56. Purchase, G.K.; Du Toit, J.T. The use of space and prey by cheetahs in Matusadona National Park, Zimbabwe. *South Afr. J. Wildl. Res.* **2000**, *30*, 139–144.
57. Broomhall, L.S.; Mills, M.G.L.; Du Toit, J.T. Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *J. Zool.* **2003**, *261*, 119–128.
58. Mills, M.G.L.; Broomhall, L.S.; du Toit, J.T. Cheetah *Acinonyx jubatus* feeding ecology in the Kruger National Park and a comparison across African savanna habitats: Is the cheetah only a successful hunter on open grassland plains? *Wildl. Biol.* **2004**, *10*, 177–186.
59. Bissett, C.; Bernard, R.T.F. Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: Is the cheetah a savanna specialist? *J. Zool.* **2007**, *271*, 310–317.
60. SAIEA: Southern African Institute for Environmental Assessment. *Strategic Environmental Assessment of Large-Scale Bush Thinning and Value-Addition Activities in Namibia*; John Meinert Printing: Windhoek, Namibia, 2016.
61. Laurenson, M.K. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *J. Zool.* **1994**, *234*, 387–408.
62. Hubel, T.Y.; Myatt, J.P.; Jordan, N.R.; Dewhirst, O.P.; McNutt, J.W.; Wilson, A.M. Additive opportunistic capture explains group hunting benefits in African wild dogs. *Nat. Commun.* **2016**, *7*, 11033. https://doi.org/10.1038/ncomms11033.
63. Soto-Shoender, J.R.; McCleery, R.A.; Monadjem, A.; Gwinn, D.C. The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. *Biol. Conserv.* **2018**, *221*, 127–136.
64. Cusack, J.J.; Dickman, A.J.; Rowcliffe, J.M.; Carbone, C.; Macdonald, D.W.; Coulson, T. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE* **2015**, *10*, e0126373.
65. Walker, E.H.; Nghikembua, M.; Bibles, B.; Marker, L. Scent-post preference of free-ranging Namibian cheetahs. *Glob. Ecol. Conserv.* **2016**, *8*, 55–57.
66. Fabiano, E.; Boast, L.K.; Fuller, A.K.; Sutherland, C. The use of remote camera trapping to study cheetahs: Past reflections and future directions. In *Cheetahs: Biology and Conservation: Biodiversity of the World: Conservation from Genes to Landscapes*; Marker, L., Boast, L.K., Schmidt-Küntzel, A., Eds.; John Fedor: London, UK, 2018; pp. 415–425.
67. Rafiq, K.; Jordan, N.R.; Meloro, C.; Wilson, A.M.; Hayward, M.W.; Wich, S.A.; McNutt, J.W. Scent-marking strategies of a solitary carnivore: Boundary and road scent marking in the leopard. *Anim. Behav.* **2020**, *161*, 115–126.
68. Caro, T. *Cheetahs of the Serengeti Plains: Group Living of an Asocial Species*; University of Chicago Press: Chicago, IL, USA, 1994.
69. Whittington-Jones, B.M.; Parker, D.M.; Bernard, R.T.; Davies-Mostert, H.T. Habitat selection by transient African wild dogs (*Lycaon pictus*) in northern KwaZulu-Natal, South Africa: Implications for range expansion. *South Afr. J. Wildl. Res.* **2014**, *44*, 135–147.

70. Mills, M.G.L.; Gorman, M.L. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol.* **1997**, *11*, 1397–1406.
71. Krüger, S.C.; Lawes, M.J.; Maddock, A.H. Diet choice and capture success of wild dog *Lycaon pictus* in Hluhluwe-Umfolozi Park, South Africa. *J. Zool.* **1999**, *248*, 543–555.
72. Malcolm, J.R.; van Lawick, H. Notes on wild dogs (*Lycaon pictus*) hunting zebras. *J. Mammal.* **1975**, *39*, 231–240.
73. Fuller, T.K.; Kat, P.W. Movements, activity, and prey relationships of Africa wild dogs (*Lycaon pictus*) near Aitong, southwestern Kenya. *Afr. J. Ecol.* **1990**, *28*, 330–350.
74. Fanshawe, J.H.; Fitzgibbon, C.D. Factors influencing hunting success of an African wild dog pack. *Anim. Behav.* **1993**, *45*, 479–490.
75. Creel, S.R.; Creel, N.M. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav.* **1995**, *50*, 1325–1339.
76. Sunquist, M.; Sunquist, F. *Wild Cats of the World*; The University of Chicago Press: Chicago, IL, USA, 2002.
77. Yoganand, K.; Owen-Smith, N. Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography* **2014**, *37*, 969–982.
78. Underwood, R. Vigilance behaviour in grazing African antelopes. *Behaviour* **1982**, *79*, 81–107.
79. Ford, A.T.; Goheen, J.R.; Otieno, T.O.; Bidner, L.; Isbell, L.A.; Palmer, T.M.; Ward, D.; Woodroffe, R.; Pringle, R.M. Large carnivores make savanna tree communities less thorny. *Science* **2014**, *346*, 346–349.
80. Riginos, C. Climate and the landscape of fear in an African savanna. *J. Anim. Ecol.* **2015**, *84*, 124–133.
81. Le Roux, E.; Kerley, G.I.; Cromsigt, J.P. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Curr. Biol.* **2018**, *28*, 2493–2499.
82. Graf, J.A.; Somers, M.J.; Gunther, M.S.; Slotow, R. Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park, South Africa. *Acta Theriol.* **2009**, *54*, 333–343.
83. Grange, S.; Owen-Smith, N.; Gaillard, J.M.; Druce, D.J.; Moleón, M.; Mgobozi, M. Changes of population trends and mortality patterns in response to the reintroduction of large predators: The case study of African ungulates. *Acta Oecologica* **2012**, *42*, 16–29.
84. Riginos, C.; Grace, J.B. Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology* **2008**, *89*, 2228–2238.
85. Kohl, M.T.; Stahler, D.R.; Metz, M.C.; Forester, J.D.; Kauffman, M.J.; Varley, N.; White, P.J.; Smith, D.W.; MacNulty, D.R. Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* **2018**, *88*, 638–652.
86. Bergstrom, B.J.; Sensenig, R.L.; Augustine, D.J.; Young, T.P. Searching for cover: Soil enrichment and herbivore exclusion, not fire, enhance African savanna small-mammal abundance. *Ecosphere* **2018**, *9*, e02519.
87. Ott, T.; Kerley, G.I.; Boshoff, A.F. Preliminary observations on the diet of leopards (*Panthera pardus*) from a conservation area and adjacent rangelands in the Baviaanskloof region, South Africa. *Afr. Zool.* **2007**, *42*, 31–37.
88. Mbizah, M.M.; Marino, J.; Groom, R.J. Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe: Implications for conservation of the African wild dog (*Lycaon pictus*). *South Afr. J. Wildl. Res.* **2012**, *42*, 94–103.
89. Fuller, T.; Sievert, P. Carnivore demography and the consequences of changes in prey availability. In *Carnivore Conservation*; Gittleman, J.L., Funk, S.M., Macdonald, D., Wayne, R.K., Eds.; Cambridge University Press: Cambridge, UK, 2001; pp.163–179.
90. Palomares, F.; Caro, T.M. Interspecific killing among mammalian carnivores. *Am. Nat.* **1999**, *153*, 492–508.
91. Lima, S.L. Putting predators back into behavioral predator–prey interactions. *Trends Ecol. Evol.* **2002**, *17*, 70–75.
92. Kavwele, C.M.; Kimanzi, J.K.; Kinyanjui, M.J. Impacts of bush encroachment on wildlife species diversity, composition, and habitat Preference in Ol Pejeta Conservancy, Laikipia, Kenya. *Int. J. Ecol* **2017**, *2017*, 1–6. https://doi.org/10.1155/2017/5620125.
93. Kiffner, C.; Rheault, H.; Miller, E.; Scheetz, T.; Enriquez, V.; Swafford, R.; Kioko, J.; Prins, H.H. Long-term population dynamics in a multi-species assemblage of large herbivores in East Africa. *Ecosphere* **2017**, *8*, e02027.
94. Schwarz, K.; Finckh, M.; Stolter, C. Influence of differently managed bush-encroached sites on the large herbivore distribution in the Namibian Savannah. *Afr. J. Ecol.* **2018**, *56*, 290–300.
95. Khorozyan, I.; Ghoddousi, A.; Soofi, M.; Waltert, M. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biol. Conserv.* **2015**, *192*, 268–275.
96. Gordon, I.J.; Prins, H.H.T. Grazers and browsers in a changing world: Conclusions. In *The Ecology of Browsing and Grazing. Ecological Studies*; Gordeon, I.J., Prins, H.H.T., Eds.; Springer: Berlin/Heidelberg, Germany, 2008; Volume 195, pp. 309–321.
97. Prins, H.H.; van der Jeugd, H.P. Herbivore population crashes and woodland structure in East Africa. *J. Ecol.* **1993**, *81*, 305–314.
98. Ogutu, J.O.; Piepho, H.P.; Said, M.Y.; Kifugo, S.C. Herbivore dynamics and range contraction in Kajiado County Kenya: Climate and land use changes, population pressures, governance, policy and human-wildlife conflicts. *Open Ecol. J.* **2014**, *7*, 9–31.
99. Hayward, M.W.; Kerley, G.I. Prey preferences and dietary overlap amongst Africa's large predators. *South Afr. J. Wildl. Res.* **2008**, *38*, 93–108.
100. Brockmann, H.J.; Barnard, C.J. Kleptoparasitism in birds. *Anim. Behav.* **1979**, *27*, 487–514.
101. Hunter, J.S.; Durant, S.M.; Caro, T.M. To flee or not to flee: Predator avoidance by cheetahs at kills. *Behav. Ecol. Sociobiol.* **2007**, *61*, 1033–1042.
102. Mills, M.G.L.; Mills, M.E.J. Cheetah cub survival revisited: A re-evaluation of the role of predation, especially by lions, and implications for conservation. *J. Zool.* **2014**, *292*, 136–141.
103. Dröge, E.; Creel, S.; Becker, M.S.; M'soka, J. Spatial and temporal avoidance of risk within a large carnivore guild. *Ecol. Evol.* **2017**, *7*, 189–199.

104. Loarie, S.R.; Tambling, C.J.; Asner, G.P. Lion hunting behaviour and vegetation structure in an African savanna. *Anim. Behav.* **2013**, *85*, 899–906.
105. Ramesh, T.; Kalle, R.; Rosenlund, H.; Downs, C.T. Low leopard populations in protected areas of Maputaland: A consequence of poaching, habitat condition, abundance of prey, and a top predator. *Ecol. Evol.* **2017**, *7*, 1964–1973.
106. Gigliotti, L.C.; Slotow, R.; Hunter, L.T.; Fattebert, J.; Sholto-Douglas, C.; Jachowski, D.S. Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. *Sci. Rep.* **2020**, *10*, 1–10.
107. Creel, S.R.; Creel, N.M. Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol.* **1996**, *10*, 526–538.
108. Gorman, M.L.; Mills, M.G.L.; Raath, J.P.; Speakman, J.R. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* **1998**, *391*, 479–481.
109. Woodroffe, R. Ranging behaviour of African wild dog packs in a human-dominated landscape. *J. Zool.* **2010**, *11*, 1–10.
110. Michel, M.J.; Adams, M.M. Differential effects of structural complexity on predator foraging behavior. *Behav. Ecol.* **2009**, *20*, 313–317.
111. Blake, L.W.; Gese, E.M. Resource selection by cougars: Influence of behavioral state and season. *J. Wildl. Manag.* **2016**, *80*, 1205–1217.
112. Hay, C.T.; Cross, P.C.; Funston, P.J. Trade-offs of predation and foraging explain sexual segregation in African buffalo. *J. Anim. Ecol.* **2008**, *77*, 850–858.
113. Trinkel, M.; Kastberger, G. Competitive interactions between spotted hyenas and lions in the Etosha National Park, Namibia. *Afr. J. Ecol.* **2005**, *43*, 220–224.
114. Stein, A.B.; Bourquin, S.L.; McNutt, J.W. Avoiding intraguild competition: Leopard feeding ecology and prey caching in northern Botswana. *Afr. J. Wildl. Res.* **2015**, *45*, 247–257.
115. Balme, G.A.; Miller, J.R.; Pitman, R.T.; Hunter, L.T. Caching reduces kleptoparasitism in a solitary, large felid. *J. Anim. Ecol.* **2017**, *86*, 634–644.
116. Yarnell, R.W.; Phipps, W.L.; Burgess, L.P.; Ellis, J.A.; Harrison, S.W.; Dell, S.; Scott, D.M. The influence of large predators on the feeding ecology of two African mesocarnivores: The black-backed jackal and the brown hyaena. *Afr. J. Wildl. Res.* **2013**, *43*, 155–166.
117. Mills, M.G. *Kalahari Hyaenas*; Unwin Hyman: London, UK, 1990.
118. Mills, M.G.L.; Funston, P.J. Large carnivores and savannah heterogeneity. In *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*; du Toit, J.T., Rogers, K.H., Bigg, H.C., Eds.; Island Press: Washington, DC, USA, 2003; pp. 370–388.
119. Dube, K.; Nhamo, G. Evidence and impact of climate change on South African national parks. Potential implications for tourism in the Kruger National Park. *Environ. Dev.* **2020**, *33*, 100485.
120. Stander, P.E. Cooperative hunting in lions: The role of the individual. *Behav. Ecol. Sociobiol.* **1992**, *29*, 445–454.
121. Brashares, J.S.; Prugh, L.R.; Stoner, C.J.; Epps, C.W. Ecological and conservation implications of mesopredator release. In *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*; Terborgh, J., Estes, J.A., Eds.; Island Press: Washington, DC, USA, 2010; pp. 221–240.
122. Salo, P.; Korpimäki, E.; Banks, P.B.; Nordström, M.; Dickman, C.R. Alien predators are more dangerous than native predators to prey populations. *Proc. Royal Soc. B Biol. Sci.* **2007**, *274*, 1237–1243.
123. Nghikembua, M.T.; Marker, L.L.; Brewer, B.; Leinonen, A.; Mehtätalo, L.; Appiah, M.; Pappinen, A. Restoration thinning reduces bush encroachment on freehold farmlands in north-central Namibia. *For. Int. J. For. Res.* **2021**, *94*, 551–564.
124. Cristescu, B.; Bernard, R.T.; Krause, J. Partitioning of space, habitat, and timing of activity by large felids in an enclosed South African system. *J. Ethol.* **2013**, *31*, 285–298.
125. Wessels, K.; Mathieu, R.; Knox, N.; Main, R.; Naidoo, L.; Steenkamp, K. Mapping and monitoring fractional woody vegetation cover in the Arid Savannas of Namibia Using LiDAR training data, machine learning, and ALOS PALSAR data. *Remote Sens.* **2019**, *11*, 2633.
126. Atkinson, H.; Cristescu, B.; Marker, L.; Rooney, N. Habitat thresholds for successful predation under landscape change. *Landsc. Ecol.* **2022**. https://doi.org/10.1007/s10980-022-01512-x.