

Habitat degradation, vegetation damage, and wildlife-livestock interactions in Amboseli ecosystem wildlife sanctuaries, Kenya

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Abstract

It is important to assess whether anthropogenic activity affects wildlife distribution and resource use to appraise the efficacy of multi-use protected areas. Habitat degradation and vegetation damage as indicators of competitive and facilitative livestock-wildlife interactions were the focus of this study. Foot transects were conducted in the dry season of 2011, wet season of 2012, and dry season of 2012 in five wildlife sanctuaries in the Amboseli ecosystem, Kenya, to determine whether habitat degradation and vegetation damage affected wildlife distribution and wildlife-livestock interactions. Simpson's and Jaccard's biodiversity indices and Pianka's niche overlap index were used to assess wildlife-livestock interactions across a gradient of habitat degradation. In the dry season, Jaccard's, Pianka's, and Simpson's indices (0.50, 0.84, and 0.99, respectively) peaked at the highest level of degradation. In the wet season, Jaccard's index (0.42) peaked at a fairly high level of habitat degradation, Pianka's index (0.82) at a fairly low level, and Simpson's (0.80) at the lowest level. Two-way ANOVA revealed that there was no effect of degradation or vegetation damage on wildlife distribution irrespective of the feeding guild. Therefore, it appears that continued shared use of the Amboseli landscape by wildlife and livestock is feasible.

KEYWORDS

Kenya, livestock, pastoralism, wildlife

Résumé

Il est essentiel de déterminer si l'activité anthropique affecte la répartition de la faune et l'utilisation des ressources afin d'évaluer l'efficacité des aires protégées à usages multiples. La dégradation de l'habitat et les dommages causés à la végétation en tant qu'indicateurs d'interactions concurrentielles ou de facilitation entre le bétail et la faune étaient au centre de cette étude. Des recensements pédestres par transects ont été effectués au cours de la saison sèche de 2011, de la saison des pluies de 2012 et de la saison sèche de 2012 au sein de cinq réserves fauniques de l'écosystème d'Amboseli, au Kenya, afin de déterminer si la dégradation de l'habitat et les dommages causés à la végétation affectaient la répartition de la faune et les interactions entre la faune et le bétail. Les indices de biodiversité de Simpson et de Jaccard et l'indice

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de chevauchement de niche de Pianka ont été utilisés afin d'évaluer les interactions entre la faune et le bétail sur un gradient de dégradation de l'habitat. Pendant la saison sèche, les indices de Jaccard, Pianka et Simpson (0.50, 0.84 et 0.99, respectivement) ont culminé au niveau de dégradation le plus élevé. Pendant la saison des pluies, l'indice de Jaccard (0.42) a culminé à un niveau assez élevé de dégradation de l'habitat, l'indice de Pianka (0.82) est resté à un niveau assez bas et celui de Simpson (0.80) a présenté le niveau le plus bas. L'ANOVA à deux facteurs a révélé que les dégradations ou les dommages causés à la végétation n'avait aucun effet sur la répartition de la faune, quelle que soit le régime alimentaire. Par conséquent, il semble que la poursuite de l'utilisation partagée de la région d'Amboseli par la faune et le bétail est réalisable.

1 | INTRODUCTION

Although considered a stronghold for megafauna, East Africa has suffered severe wildlife declines in recent decades (Romanach et al., 2007). Therefore, protected areas have been set up across the region that explicitly forbids human encroachment or natural resource extraction in the interest of wildlife protection and ecotourism (Packer et al., 2013). However, there has been a paradigm shift in wildlife conservation in recent years, transitioning from protected areas that isolate wildlife from people towards multi-use landscapes that are intended to meet the needs of both (Dheer et al., 2021; Kesch et al., 2015). The wildlife sanctuaries in Kenya's Amboseli ecosystem serve as an example of the latter. This type of land use involves local communities in the decision-making process and aims to maintain the sanctuaries as important tracts for wildlife dispersal and migration. Furthermore, the sanctuaries act as a buffer between Amboseli National Park and the surrounding human communities by providing a geographical boundary.

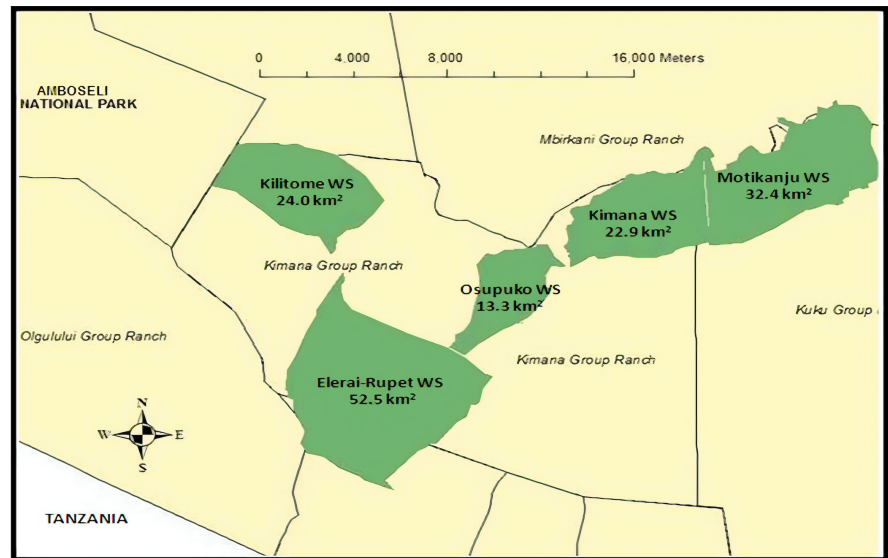
Despite the logical reasons for establishing wildlife sanctuaries, there is little research published on their ecological efficacy and ability to protect wildlife (Okello, 2005). Wildlife sanctuaries have suffered from mismanagement and inefficient oversight, which has limited their conservation potential (Okello et al., 2011; Okello & Kiringe, 2004). Further research is required to understand the needs of wildlife in multi-use sanctuaries and the sustainability of current livestock grazing plans. Several challenges face the management of wildlife sanctuaries in the Amboseli ecosystem, including human population growth, human-wildlife conflict, division of group ranches, agricultural expansion, and natural resource depletion (Okello et al., 2011). In addition, habitat degradation and vegetation damage due to livestock overgrazing have become increasingly problematic. Overgrazing leads to soil erosion and compaction, vegetation trampling and loss, proliferation of invasive woody plants, and water body sedimentation (Homewood & Rodgers, 1987). Habitat degradation and vegetation damage have increased in these sanctuaries over time (Mwasi & Acker, 2015).

The potential of Amboseli ecosystem wildlife sanctuaries to serve as dispersal areas for wildlife is contingent on sustainable use

by humans and livestock (Okello, 2009). There was evidence of partitioning in habitat selection between livestock and wildlife in the Amboseli ecosystem during the wet season (Mwasi & Fisher, 2018). Accounting for these seasonal differences, it was suggested that seasonal grazing plans be established in the sanctuaries. A rotational, nomadic grazing system for livestock whereby there is spatial partitioning between livestock and wildlife in order to mitigate the negative effects of overgrazing was suggested in another study (Sitters et al., 2009). This form of spatial partitioning would theoretically meet the needs of pastoral communities while allowing for wildlife persistence, ultimately benefiting both. It would also lead to reduced habitat degradation owing to diffusion of grazing impacts. A grazing plan that accounts for both temporal and spatial factors may lead to sustainable coexistence between livestock and wildlife in the Amboseli ecosystem according to the above studies.

The key to understanding the facilitative and competitive interactions between livestock and wild herbivores – and the factors that drive them – is an examination of niche differentiation and functional resource heterogeneity (Fynn et al., 2016). In Australia, livestock grazing and subsequent habitat loss affected wildlife habitat selection in Australia, which in turn reduced access to foraging sites (Maron & Lill, 2005). Grevy's zebra (*Equus grevyi*) in Kenya avoided high-traffic livestock areas and preferred to forage in areas distant from livestock corrals, which reduced the nutritional quality of the grass consumed (Sundaresan et al., 2008; Williams, 1998). Proximity to villages and the size of cattle pastures had pronounced effects on wildlife dispersal and species richness in arid Botswana (Wallgren et al., 2009). There was a pronounced increase in vegetation damage across multiple field sites in eastern and southern Africa in areas where livestock replaced wildlife (Werger, 1977). Despite the seemingly negative impacts of both livestock and habitat degradation on wildlife populations, there are research findings that suggest coexistence is possible. Competition may in fact be seasonal rather than year-round (Myserud, 2000; Voeten & Prins, 1999). With regards to degraded habitats, several studies have shown that wildlife may in fact thrive in degraded areas or human-dominated landscapes (Abay et al., 2011; Prange et al., 2003; Soulsbury & White, 2016). Therefore, there are mixed results on how habitat

FIGURE 1 Location of the study area in the Amboseli ecosystem of Kenya (Source: Mwasi & Fisher, 2018)



degradation affects wildlife habitat use and whether it is a driver of wildlife-livestock conflict or competitive exclusion. With a sound understanding of these concepts, wildlife managers can implement strategies that maximise structural heterogeneity of grasslands, thereby minimising the competition between livestock and wildlife (Fynn et al., 2017).

The influence of habitat degradation and vegetation damage levels on livestock-wildlife interactions is accordingly important to study. There is a paucity of published studies focused on how these factors affect wildlife resource selection and whether wildlife of different feeding niches may respond differently to livestock pressure. The overarching aim of this study was therefore to determine how habitat degradation and vegetation damage affect wildlife resource selection and livestock-wildlife interactions in the Amboseli ecosystem's wildlife sanctuaries. If higher levels of degradation lead to altered habitat selection or avoidance of livestock by wildlife, there is clear evidence of competitive exclusion of wildlife by livestock. The objectives of this study were (i) to assess how the extent of habitat degradation and vegetation damage impacted habitat use and distribution of herbivores of different feeding classes and (ii) to determine how habitat degradation, vegetation damage, and season influenced wildlife-livestock interactions. Specifically, based on a thorough review of previous studies within sub-Saharan Africa (see Fynn et al., 2016), we developed the following predictions on the effects of habitat degradation on wildlife and wildlife-livestock interactions:

1. Tall-grass specialists are vulnerable to competitive exclusion and would be limited by the presence of livestock and/or the effects of livestock (e.g. vegetation damage and degradation)
2. Short-grass specialists will either be facilitated by or at least not limited by the presence and/or effects of livestock.
3. The Amboseli ecosystem, being a medium-productivity savanna, would feature competitive exclusion during the dry season but not the wet season.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in five wildlife sanctuaries located in the Amboseli ecosystem: Elerai-Rupet, Kilitome, Kimana, Motikanju, and Osupuko. Kilitome sanctuary directly borders Amboseli National Park (Figure 1). These sanctuaries together form the Kimana Wildlife Corridor. They provide critical dispersal and corridor habitats for Amboseli National Park's wildlife. The area experiences a typical East African rainfall pattern, with short rains occurring from November to January and long rains occurring from March to May. Mean annual rainfall is approximately 569 mm, though it has declined since the 1960s (Aduma et al., 2018). Temperatures usually range from 12°C in July to 35°C in February with an average of 21–25°C each month (Worden et al., 2003). These sanctuaries are mostly dominated by thorny *Acacia* spp. and *Balanites glabra* in bushland and woodland plant communities, and spear grass (*Heteropogon contortus*) in grassland. Soils in the Amboseli ecosystem are ill-suited to agriculture and intensive grazing due to low nutrient content and poor drainage. Soil types range from shallow volcanic andisols, black cotton soils, ash soils, dark red sandy loams, to black clay soils (Okello & Kiringe, 2008). Despite this, both agriculture and livestock grazing have increased with time in the ecosystem.

2.2 | Sampling design and field data collection procedures

To ensure adequate sample size and replication, five wildlife sanctuaries in the Kimana wildlife corridor, which forms a significant proportion of the Amboseli ecosystem, i.e. Elerai-Rupet, Kilitome, Kimana, Motikanju, and Nailepo, were sampled. Each sanctuary was considered a focal data collection site for this study. A

sanctuary was sampled 10 times each season ($n = 10$). Therefore, the total number of replications for the ecosystem was 50. Data were collected from each sanctuary for a complete typical annual seasonal cycle comprising of three seasons: dry season of 2011, followed by the succeeding wet season of 2012, and finally the dry season of 2012.

A sampling unit was defined as a single foot transect within each sanctuary. A total of 54 transects were sampled across the five wildlife sanctuaries as follows: Elerai-Rupet (12), Kilitome (8), Kimana (9), Motikanju (8), Nailepo (11) and Osupuko (6). Foot transects oriented in a north-south or south-north direction covering at least 40% of each sanctuary's total area were designated prior to fieldwork using ArcGIS 9 software. Starting points of the first transects were randomly chosen. Buffers were walked in a perpendicular direction of each transect depending on the original orientation of the transects. The maximum perpendicular sighting distances were used to determine the buffer width by multiplying that distance by three. This was done to ensure that wildlife was not double-counted (Mwasi & Fisher, 2018).

Each time wildlife was sighted, details including the UTM coordinates of their location, habitat type, species, and group composition were recorded. The coordinates were determined by adding the easting and northing from the transect start point to the location where wildlife was observed. Only livestock (cattle, goat, and sheep) and wildlife larger than the dik dik (*Madoqua kirkii*) were considered in this study. At each sighting event of wildlife and/or livestock, a 10 × 10 m area was inspected to assess and score the respective degradation level and vegetation damage.

Habitat types were classified following the Pratt and Gwynne (1977) physiognomic classification guide. Woodland was characterised as a tract of land supporting trees up to 20 m in height, shrubland up to 6 m in height, and bushland as an assemblage of trees and shrubs. Grassland contained only grasses sometimes interspersed with small shrubs.

At each sighting event, bare ground cover clearly ascertained to have resulted from adverse human or livestock disturbances or a combination of both was used as a proxy for habitat degradation. Bare ground cover was given a score from 1 (no bare ground) to 4 (completely bare ground). Vegetation damage (a proxy for foraging intensity, i.e. grazing/browsing intensity) was assessed based on the extent of overgrazed or shortly-cropped grass, damaged bushes, and/or broken/debarked tree and shrub branches and given a similar rating from 1 to 4. Therefore, each site received two scores: one for habitat degradation and another for vegetation damage.

2.3 | Data analyses

All statistical analyses were conducted in R version 4.0.3 (R Core Team, 2020). The package 'stats' (R Core Team, 2019) was used for conducting statistical tests (e.g. ordinary linear regression, or OLS, and analysis of variance, or ANOVA), 'dplyr' (Wickham

et al., 2019) was used for filtering and sorting the datasets, 'ggplot2' (Wickham, 2016) was used for creating plots, and 'plotrix' (Lemon, 2006) was used to compute standard errors. Unless stated otherwise, $\alpha = 0.05$ was deemed significant and all mean values are displayed with standard errors.

An ordinary least-squares regression (OLS) model was run to test whether the livestock abundance (independent variable) at a given site limited the wildlife abundance (dependent variable) at the same site. A Wilcoxon test was also used to assess whether the season (dry or wet) influenced the mean degradation and vegetation damage scores. For the OLS, the distribution of residuals did not significantly deviate from normality (Shapiro-Wilk tests) and variances were homoscedastic (Breusch-Pagan tests and residuals plots; R package 'car'; Fox & Weisberg, 2011).

Three commonly applied statistical indices of resource use similarity, niche overlap, and biodiversity were used to explore how these different factors varied according to the degradation level and season. We calculated Jaccard's similarity index (Mueller-Dombois & Ellenberg, 1974) using package 'jaccard' (Chung et al., 2018) to compare similarity of use of sites by both livestock and wildlife using the following formula:

$$S = \frac{A}{A + B + C}$$

where S is the similarity index from 0 (no similarity) to 1 (total similarity), A is the number of sites with both livestock and wildlife, B is the number of sites with only wildlife, and C is the number of sites with only livestock.

We used Pianka's index of niche overlap (Pianka, 1973) to assess habitat use overlap between livestock and wildlife based on the degradation level and season using the following formula:

$$O = \frac{\sum p1 * p2}{\sqrt{\sum p1^2 * \sum p2^2}}$$

where O is the index of overlap, with a minimum of 0 (indicating no overlap) and a maximum of 1 (indicating complete overlap), $p1$ is the proportion of livestock within a given habitat, and $p2$ is the proportion of wildlife within a given habitat.

Simpson's diversity index (Simpson, 1949) was used to determine wildlife species diversity based on the three categories of degradation levels and the season (package 'vegan'; Oksanen et al., 2020). The following formula was used:

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$$

where D is the species diversity index with a minimum of 0 (i.e. only one species occurs at the given category) and a maximum of 1 (infinite diversity), n is the number of individuals of a particular species, and N is the number of individuals of all species. Jaccard's similarity index, Pianka's index of niche overlap, and Simpson's diversity index were calculated separately for the dry and wet seasons to assess whether

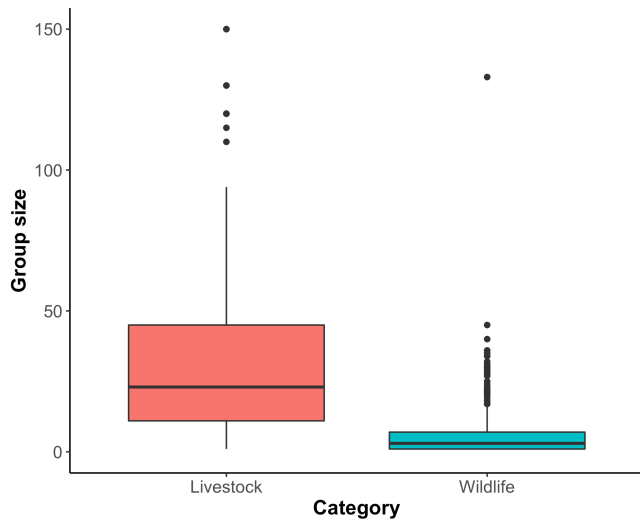


FIGURE 2 Mean group size for wildlife and livestock sightings in this study

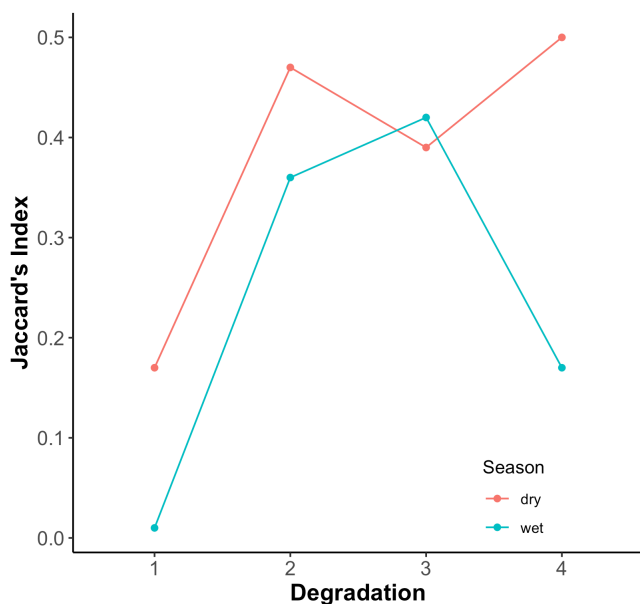


FIGURE 3 Jaccard's similarity index in site usage by livestock and wildlife according to the season and degradation score

these indicators of similarity, overlap, and diversity, respectively, differed with seasons. All three have been established as rigorous and sound methods for assessing similarity in resource use, niche overlap, and biodiversity as they relate to different species of wildlife and/or livestock [e.g. for Jaccard's similarity index: Kittur et al. (2010); for Pianka's index of niche overlap: Hemami et al. (2004); for Simpson's diversity index: Bibi & Ali (2013)].

Finally, following appropriate goodness-of-fit testing (as in Hidalgo et al., 2018), a set of two-way ANOVAs was run to assess how degradation level and vegetation damage influenced the distribution (i.e. raw abundance count) of wildlife of five different feeding guilds: tall grazers, short grazers, browsers, mixed feeders, and miscellaneous. Following the ANOVA, Tukey post-hoc tests were run

to establish where the differences (if any) lay. Feeding guilds were categorised such that tall grazers included African buffalo (*Syncerus caffer*) and plains zebra (*Equus quagga*), short grazers included wildebeest (*Connochaetes taurinus*), reedbuck (*Redunca redunca*), the common warthog (*Phacochoerus africanus*), waterbuck (*Kobus ellipsiprymnus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella rufifrons*), African savanna hare (*Lepus microtis*), mixed feeders included the African bush elephant (*Loxodonta africana*), common eland (*Taurotragus oryx*), impala (*Aepyceros melanus*), and bushbuck (*Tragelaphus scriptus*). Wildlife browsers included the Maasai giraffe (*Giraffa camelopardalis tippelskirchii*), gerenuk (*Litocranius walleri*), Kirk's dik dik (*Madoqua kirkii*), steenbok (*Raphicerus campestris*), greater kudu (*Tragelaphus strepsiceros*), and lesser kudu (*Tragelaphus imberbis*). Finally, a catch-all category of miscellaneous feeders included the olive baboon (*Papio anubis*), black-backed jackal (*Canis mesomelas*), vervet monkey (*Chlorocebus pygerythrus*), banded mongoose (*Mungos mungo*), bat-eared fox (*Otocyon megalotis*), and rock hyrax (*Procavia capensis*). While the miscellaneous feeders are not in direct competition for resources with livestock, they formed a control group to contrast with the other ungulate-dominated feeding guilds and were therefore included in the analysis in their own category.

3 | RESULTS

Of the 54 sampling sites, the majority ($n = 36$) had both wildlife and livestock, followed by those that had only wildlife ($n = 12$) and then those that had only livestock ($n = 6$). There were 884 combined sightings of wildlife ($n = 674$ sightings) and livestock ($n = 210$ sightings). Although livestock had fewer total sighting events than wildlife, group size for livestock was 39.95 ± 3.17 and for wildlife 5.36 ± 0.31 (Figure 2). In total, we counted 8390 livestock and 3613 wildlife. OLS revealed that wildlife abundance was not affected by livestock abundance ($r^2 = 0.03$, $p = 0.10$). 11 habitat types were recorded in total: bush grassland, bushland, shrubland, shrub grassland, grassland, wooded grassland, forest, woodland, dwarf shrubland, riverine, and rocky outcrop. There was a significant difference (Wilcoxon test; $W = 107,718$, $p < 0.001$) in habitat degradation levels for wet (mean: 2.35 ± 0.06) and dry (mean: 2.92 ± 0.04) seasons. In contrast, there was no significant difference ($W = 84,568$, $p = 0.14$) in vegetation damage levels for the wet (mean: 1.83 ± 0.05) and dry (mean: 1.92 ± 0.03) seasons.

3.1 | Similarity

In the dry season, Jaccard's similarity index peaked at the highest level of degradation (0.50) and was lowest at the lowest level of degradation (0.17; Figure 3). The wet season showed a different trend, with Jaccard's index peaking at the second highest level of degradation (0.42), followed by the second lowest (0.36), but again being lowest at the lowest level (0.01; Figure 3).

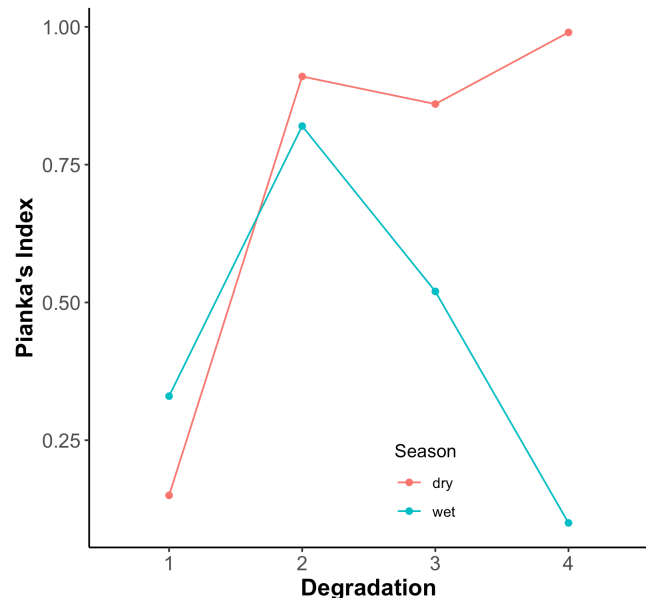


FIGURE 4 Pianka's index of niche overlap between wildlife and livestock based on season and degradation level

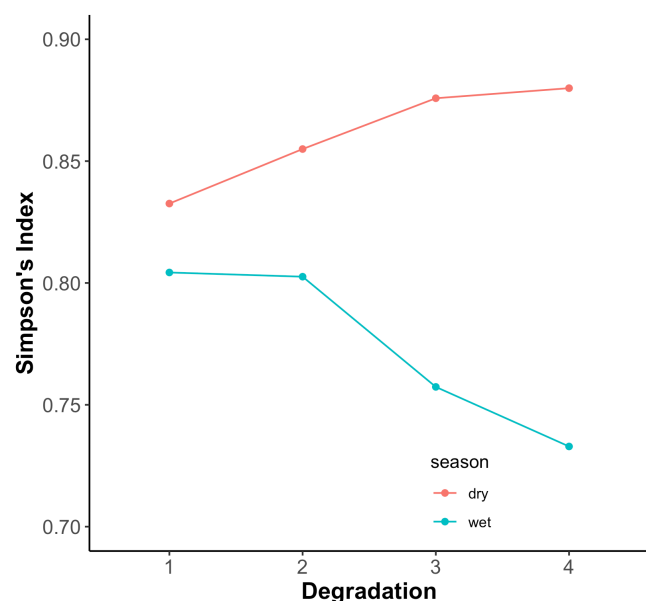


FIGURE 5 Simpson's diversity index based on season and degradation level

3.2 | Niche overlap

Pianka's index of niche overlap between livestock and wildlife showed disparate patterns between the seasons. In the dry season, niche overlap increased with increasing degradation, being lowest (0.15) at a degradation level of 1 and peaking (0.99) at a degradation level of 4 (Figure 4). In contrast, during the wet season, niche overlap peaked at a degradation level of 2 (0.82) but then declined until a degradation level of 4 (index of 0.10).

3.3 | Diversity

In the dry season, Simpson's diversity index increased with increasing levels of degradation (level 1: 0.83, level 4: 0.88; Figure 5). Conversely, during the wet season, diversity reduced with increasing levels of degradation (level 1: 0.80, level 4: 0.73). Diversity was higher during the dry season than at any point during the wet season. Regardless, diversity was fairly high across all four levels of degradation irrespective of season, not showing the wide range seen with similarity (Figure 3) or overlap (Figure 4).

3.4 | Feeding guilds

Two-way ANOVA revealed a complete lack of effect of habitat degradation and vegetation damage on the abundance of members of the different feeding classes. First, the distribution of browsers was not influenced by degradation level [$F(3, 84) = 0.33, p = 0.81$] or vegetation damage [$F(3, 84) = 0.55, p = 0.65$]. Short grazers were also not affected by either degradation [$F(3, 337) = 1.51, p = 0.21$] or vegetation damage [$F(3, 337) = 0.34, p = 0.80$]. Results for tall grazers showed the same relationship [degradation: $F(3, 87) = 0.98, p = 0.41$]; vegetation damage: [$F(3, 87) = 1.13, p = 0.34$], as well as for mixed feeders (degradation: [$F(3, 96) = 0.93, p = 0.43$]; vegetation damage: [$F(2, 96) = 0.07, p = 0.93$]). Miscellaneous feeders were also not influenced by either degradation: [$F(3, 24) = 0.54, p = 0.66$] or vegetation damage [$F(3, 24) = 0.27, p = 0.85$].

4 | DISCUSSION

Overall, the results demonstrate that livestock grazing and pastoralist activity are potentially sustainable and do not necessarily displace wildlife in the Amboseli ecosystem wildlife sanctuaries. There was no overall effect of livestock abundance on wildlife abundance, and there was similarly no effect of habitat degradation or vegetation damage on wildlife abundance irrespective of feeding guild.

While these results may be surprising at first, it may be due to the fact that both livestock and wildlife both preferentially fed in areas with attractive abiotic and biotic factors. The areas with low degradation levels may have had poorer quality soils and forage and/or high predator occupancy that might have lowered their usage by wild herbivores, and a stronger suppressive effect than the livestock did. Highly degraded (i.e. high livestock traffic) areas may also be key sources of fresh water in the dry season, making them important areas for wildlife as well. Across sub-Saharan Africa, herbivores congregate at water sources during the dry season (Thrash et al., 1995), and in general, their migration pattern is closely tied to water availability (Coe et al., 1976). Furthermore, large carnivores often congregate in areas where there is limited human activity (Brackowski et al., 2022; Dheer et al., 2022), possibly leading to ungulate prey – which were the subject of this study – avoiding such areas (Davidson et al., 2019; Valeix et al., 2009).

Despite these findings, the patterns observed in Pianka's niche overlap and Simpson's diversity indices may be predictive of future competitive exclusion of wildlife by livestock. Diversity peaked at very high and very low levels of degradation during the dry and wet seasons, respectively. These contrasting seasonal patterns suggests that resource pulses may be driving the movements of wildlife and livestock in the Amboseli ecosystem. During the dry season, wildlife may be forced to congregate in areas of high livestock use (i.e. highly degraded areas) to access forage and water. Niche overlap peaked at the highest levels of degradation during the dry season, but was lowest during the wet season. This further suggests that there may be seasonal differences in livestock and wildlife movement patterns and foraging behaviour, placing them at increased risk of competition during the dry season. Although the results from the OLS and ANOVA tests did not detect any significant effects, it is plausible that, as livestock activity increases in the future, wildlife will be limited by livestock during the dry season.

The results may also suggest a certain level of behavioural plasticity in wildlife that allows them to coexist alongside livestock. For example, a meta-analysis conducted by Gaynor et al. (2018) found that wildlife species adjust their activity patterns as a response to anthropogenic activity. The activity patterns of herbivores in this heavily grazed area may therefore be influenced by livestock and human presence during the daytime. The distinct trends observed in Pianka's index across the seasons are not surprising, because the index is calculated based on how evenly spread individuals of different species are at different sites. Moderately degraded areas may serve as a balance between areas of optimal foraging and areas that are highly degraded for all species to thrive in the wet season, as a study in Uganda found (Rannestad et al., 2006). In this study, as with Mwasi and Fisher (2018), there appears to be some evidence of competitive exclusion in more highly degraded areas during the dry season. Such areas may have important water sources. All four levels of degradation hosted species of different feeding guilds, but the fewest number of species ($n = 10$) were observed at high levels of degradation, which reflects that there may exist a critical threshold of degradation where species diversity is diminished.

The lack of differences observed in the distribution among the wildlife feeding guilds indicates that class-level effects may not be distinguishable in our study area yet. This finding is accordingly relevant to single- and multi-species conservation efforts and demonstrates the importance of allowing for different categories with the analysis. While sample sizes for this study did not allow for analyses of each individual species, the inclusion of different feeding guilds paves the way for additional longitudinal studies that model how distribution may change over time and as disturbance increases. Whenever possible, group or individual-level analyses should be conducted to detect species or guild level differences that could otherwise be overlooked. The relative impacts and needs of different feeding guilds in an ecosystem are not always uniform (Andrew & Hughes, 2005) due to dietary niche partitioning (Kartzinel et al., 2015). For example, if an ungulate of high conservation priority, e.g. the Grevy's zebra of northern Kenya,

is being competitively excluded by livestock (as demonstrated by Low et al., 2009), the effect may be masked if all wildlife are considered collectively. Thus, it makes sense to look at how different levels of resource exploitation via livestock feeding may or may not impact different wildlife feeding guilds. To that end, however, it is apparent that our predictions on the differences in the grazer feeding guilds (i.e. short and tall grass grazers) did not hold true and that the pressure incurred by wildlife by livestock grazing in the Amboseli ecosystem is not too severe yet.

Altogether, this study highlights the potential for shared resource use between humans, their livestock, and wildlife in the Amboseli ecosystem, though we suggest long-term monitoring to detect changes in the measures we examined. It may be prudent to adapt coexistence strategies according to the season. Our study also demonstrates the complexity of managing this diverse ecosystem, which is home to multiple herbivorous feeding guilds and a strong seasonal pattern of precipitation. The findings will be useful to wildlife managers working in multi-use landscapes who are seeking to balance the needs of pastoralists and wildlife.

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CONFLICT OF INTEREST

The authors do not declare any conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available upon reasonable request from the corresponding author.

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