Top–down limits on prey populations may be more severe in larger prey species, despite having fewer predators

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Variation in the vulnerability of herbivore prey to predation is linked to body size, yet whether this relationship is size-nested or size-partitioned remains debated. If size-partitioned, predators would be focused on prey within their preferred prey size range. If size-nested, smaller prey species should become increasingly more vulnerable because increasingly more predators are capable of catching them. Yet, whether either of these strategies manifests in top–down prey population limitation would depend both on the number of potential predator species as well as the total mortality imposed. Here we use a rare ecosystem scale 'natural experiment' comparing prey population dynamics between a period of intense predator persecution and hence low predator densities and a period of active predator protection and population recovery. We use three decades of data on herbivore abundance and distribution to test the role of predation as a mechanism of population limitation among prey species that vary widely in body size. Notably, we test this within one of the few remaining systems where a near-full suite of megaherbivores occur in high density and are thus able to include a thirtyfold range in herbivore body size gradient. We test whether top–down limitation on prey species of particular body size leads to compositional shifts in the mammalian herbivore community. Our results support both size-nested and size-partitioning predation but suggest that the relative top–down limiting impact on prey populations may be more severe for intermediate sized species, despite having fewer predators than small species. In addition we show that the gradual recovery of predator populations shifted the herbivore community assemblage towards large-bodied species and has led to a community that is strongly dominated by large herbivore biomass.

Introduction

Body mass largely shapes an herbivorous species' vulnerability to predation (Hopcraft et al. 2010). However, there are essentially two competing arguments about the nature of this relationship between body size and vulnerability. The size-partitioning strategy postulates that predators target prey species within a certain preferred size range. Prey larger than the preferred size become too difficult or dangerous to subdue, while the low nutritive reward obtained from prey smaller than the preferred size does not justify the energy expense required to catch them (Rosenzweig 1966). Alternatively, the potential prey base of large predators may be more diverse than that of smaller predators because they are able to capture both large and small prey, whereas small predators are limited to catching only small prey. This size-nested strategy postulates that even if each predator has a preferred prey size range, they will opportunistically catch prey of smaller than preferred size (Sinclair et al. 2003). Thus, while large prey can only be killed by large predator species, small prey can potentially be caught by a greater number of predator species (Cohen et al. 1993, Clements et al. 2014), and thus the potential for predation to limit populations may be greater for small prey species.

The realized top–down impact on prey populations depends not only on the number of potential predators, but also on the total mortality inflicted by each predator and the magnitude of the lost potential for population recruitment of each prey species (Owen-Smith and Mills 2008a). Larger species tend to have lower recruitment rates and thus a single mortality event may have a more severe impact on their population dynamics, particularly if the animal being removed from the population still had a high potential to contribute to population growth e.g. prime-aged females (Gaillard et al. 2000, Gaillard and Yoccoz 2003). Thus, because of the more severe limitation on potential growth rates, predators may also limit populations of large animals, particularly if prey selection is size-partitioned. However, ungulates ranging in size from the 48 kg impala *Aepyceros melampus* to the 520 kg buffalo *Syncerus caffer* (average female body weight taken from Owen-Smith 1988) exhibit very similar birthing intervals linked to the seasonal cycle (Estes 1991, Ryan et al. 2007) with each normally producing only a single offspring (apart from warthog *Phacochoerus africanus* for which a litter of 3 is the norm; Mason 1982). On the other hand, the very largest herbivores with the slowest recruitment rates become too large as adults for predators to hunt successfully and tend to be mostly invulnerable to non-human predation. These very large herbivores are referred to as megaherbivores, species that exceed 1000 kg (Owen-Smith 1988) and include elephant *Loxodonta africana* (x♀ 2800–x♂ 5000 kg), white rhino *Ceratotherium simum* (x♀ 1600–x♂ 2200 kg), black rhino *Diceros bicornis* (x♀ 1080–x♂ 1124 kg), hippopotamus *Hippopotamus amphibius* (x♀ 1350–x♂ 1500 kg) and large giraffe individuals *Giraffa camelopardalis* (x♀ 825–x♂ 1200 kg; weight estimates obtained from Owen-Smith 1988). Instead, megaherbivore populations are more likely to be food limited and as such have the potential to greatly impact plant communities and vegetation structure (Owen-Smith 1988).

Vulnerability is further influenced by habitat structure as it relates to visibility. Lower visibility brought about by dense vegetation or topography could intensify predation risk by facilitating hunting success by ambush predators (Elliott et al. 1977, Hopcraft et al. 2005, Valeix et al. 2009). Yet depending on the anti-predatory strategy of the particular prey species involved, reduced visibility may also provide prey concealment. Thus, spatial variation in woody cover and temporal changes in woody thickening (defined here as an increase in either density or biomass of woody shrubs and trees) may intensify top–down control for some herbivore species while alleviating it for others.

The theoretical formulation of top–down forces limiting populations of different-sized species, is well established in the ecological literature (Hopcraft et al. 2010, Leroux and Loreau 2015). However, the landscape-level consequences are seldom demonstrated in a natural setting, particularly for large terrestrial herbivores (but see Hopcraft et al. 2012) in systems that retain functional densities of megaherbivores. In this study we have the rare opportunity to use a 'natural experiment', where historical persecution of predators and subsequent population restoration have resulted in distinct periods of low and rapidly increasing predation pressure. We test the extent to which recovering populations from two different-sized predators (wild dog *Lycaon pictus*, and lion *Panthera leo*) and spatiotemporal variation in predation risk limit prey populations and how this leads to predictable shifts in the large mammal herbivore community. This study is uniquely situated in one of the few remaining systems where megaherbivore species remain at functionally relevant densities. The few empirical examples in the literature showing the role of top–down limitation in structuring ungulate communities are from systems from which megaherbivores have long since gone locally extinct or have been drastically reduced in number. We use three decades of species' distribution data from species that range more than thirtyfold in body mass, restricting our analysis to species that include a large proportion of grass in their diet, including: the megaherbivore white rhino, buffalo, plains zebra *Equus quagga*, blue wildebeest *Connochaetes taurinus*, nyala *Tragelaphus angasii*, impala and warthog.

We predicted that: 1) the population dynamics of small species will respond to changes in the abundance of both lion and wild dog, while the population dynamics of large prey species will respond only to changes in the abundance of lion. Changes in megaherbivore populations will be unrelated to changes in predator populations; 2) the relative influence of predation risk (as estimated by surrounding visibility) on population limitation would increase as prey body size decrease; 3) as predator populations recover, the herbivore community assemblage will consist increasingly of larger-bodied species.

Material and methods

The study was performed in a roughly 900 km² fenced protected area (Hluhluwe-iMfolozi Park, hereafter HiP) in South Africa. HiP spans the gradient from semi-arid to mesic savanna with rainfall between 570 mm yr⁻¹ in the south to 950 mm yr⁻¹ in the north. The vegetation is structurally diverse, ranging from closed woodlands to grasslands (Howison et al. 2017). Historical persecution of predators ensured low predator numbers for most of the 20th century (Somers et al. 2017). Lions went locally extinct in the late 1930s and African wild dog in the mid-1940s, and restoration attempts only began in the mid-1960s and early 1980s, respectively. The wild dog population fluctuated between 5 and 28 individuals until roughly 2002, after which it increased to 109 individuals by 2011, declining to approximately 70 by 2015. The lion population fluctuated between 60 and 80 animals between 1986 and 1997. Since then the population increased to 120 by 2015 (Somers et al. 2017). Less is known about the historical densities of hyaena *Crocuta crocuta*, leopard *Panthera pardus* and cheetah *Acinonyx jubatus*.

Although elephants are present in HiP (reintroduced in 1981 after an absence of 91 yr), we excluded them from this analysis because they are censused differently. The abundance and distribution of herbivores other than elephants, have been monitored via dry season ground counts since 1986, along a series of 24 line transects with a consistent methodology (Fig. 1, see also Cromsigt et al. 2009 and Le Roux et al. 2017 for details on the transect method). Transect counts were available for approximately 70% of the park for 1986, 1987, 1988 and 1991 and biennially from 1994 onward. We excluded the remaining 30% of the park which is managed as wilderness area, where data availability and collection strategies varied. We delineated 11 sections (39–65 km²), each enclosing two to three transects (Fig. 1) and amalgamated observations across 2–3 successive censuses into 4–5 yr periods in order to have enough observations to reliably estimate herbivore abundance using distance sampling techniques (Burnham et al. 1980). We calculated per-capita rates of herbivore population change as $((D_{t2} - D_{t1})/(D_{t1} + 1))/y$ with D as the distance-derived abundance estimate per species per period and y as the interval in years between t1 and t2.

We used predator density (wild dog and lion) as an index of predation pressure. Wild dog numbers prior to 1992 and lion numbers throughout were available as an annual park-wide estimate and for these data we assumed an even park-wide distribution. From 1992, all wild dog packs were closely followed through GPS tracking. Using the number of adults and yearlings per pack and the 50% kernel utilization density, we calculated an annual wild dog density per section, considering the degree to which each section was included in one or more home ranges. Estimates were unavailable for 5 yr (1994/1995, 1995/1996, 1996/1997, 2010/2011, 2011/2012). We estimated population size during these missing years by assuming linear population change between the previous known estimate and the following known estimate. For wild dog and lion, we firstly averaged the annual density
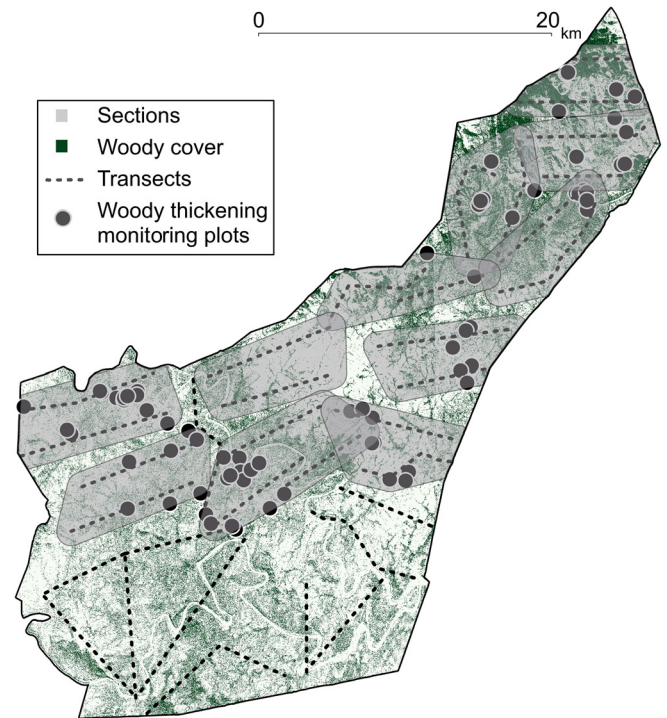

Figure 1. Map of Hluhluwe-iMfolozi Park and the 11 sections with the transects used, showing the proportion of woody cover. The locations of the 77 fixed plots in which woody thickening has been quantified are indicated by the filled circles.

per period and as a second (alternative) variable we averaged the annual densities over the same number of years per period but with a one year time lag.

Ambush predators such as lion have higher hunting success in areas of dense cover (Elliott et al. 1977, Davies et al. 2016) and, in HiP, the same has been suggested for wild dog (Krüger et al. 1999). Hence we used woody cover as a proxy for predation risk. We calculated a percentage woody cover per section (Fig. 1) using a 0.5 m resolution map of woody cover created using Google Earth images (26 March 2014 for iMfolozi and 8 May 2014 for Hluhluwe; Veldhuis et al. 2017). Based on visual inspection, a greenband threshold value of 95 was used to split woody cover from non-woody cover (Veldhuis et al. 2017 for further details). To get a measure of woody thickening over time we used data from 77 0.25-ha fixed plots in which woody cover had been quantified in 1999, 2001, 2007 and 2017 (Fig. 1). We calculated a linear rate of change in woody plants per plot over this 18 yr period, and averaged across all plots that occurred within a section. These fixed plots represented all but one of our 11 sections, thus this section was omitted from all analyses testing woody change over time, and re-added when woody thickening no longer remained in the model. As slope may also either conceal or reveal approaching predators, we also calculated the positive topographic openness in QGIS 3.0 using a 50 m resolution digital elevation model. Positive topographic openness is a measure of curvature that incorporates the terrain line of sight (Yokoyama et al. 2002).

We used monthly rainfall measurements from the three rainfall stations with the most complete records for the three decades for which we had herbivore census records. Only 15% of the annual records were missing monthly rainfall estimates, and less than 5% were missing more than 3 months yr^{-1}. We replaced these missing monthly records with the average for that month recorded over the 30-yr period at that station (no station missed more than 5 records out of the 30 potential records). We estimated temporal rainfall variation by calculating a park-wide annual average rainfall and averaged this per period. In HiP rainfall varies spatially following changes in elevation (Balfour and Howison 2002). Hence we used an elevation-weighted interpolation of rainfall to estimate spatial variation. This interpolation was produced at a 250 m resolution using monthly rainfall recorded between 2001 and 2007 at 17 rainfall stations throughout the park (Howison et al. 2017). We standardized the spatial rainfall estimate such that the values represented the proportion above or below average rainfall received by that section relative to the rest of the park. We then devised a rainfall index as the product of the temporal and spatial estimates, such that the lowest index values represent the driest regions during the driest times and vice versa.

Statistical analyses

We performed all analyses in R (R Development Core Team) and standardized all explanatory variables to facilitate comparison. We used linear mixed effects models (R package nlme, Pinheiro et al. 2016), to test if per-capita rates of population change shifted in response to predator population recovery. We regressed the per-capita rate of population change per species in each of the 11 sections for the 7 periods against the rainfall index, the proportion of woody cover per section, the average rate of woody thickening between 1999 and 2017, the average lion density and the average wild dog density (Table 1 for the structure of the full model). For both lion and wild dog we separately tested the two abundance variables (one with the one year lag and one without) and retained the variable that explained most variation in a full model. If both predator variables were retained in the Best Adequate Model (BAM), we combined the densities into a single 'predator density' variable. Positive topographic openness and woody cover were co-linear with variance inflation factors (VIF) of greater than 6, thus these variables were also tested separately. We set the sections as random term and incorporated a continuous first-order autoregressive correlation term specifying temporal dependence within each section. Spatial dependence was largely dealt with by having section defined as a random term thereby setting a compound correlation between all observations from the same section (Zuur et al. 2009, although this approach does not take into account the relative distances between sections). We checked for homogeneity of variance both visually and statistically using a variance test (Zuur et al. 2009). Where appropriate we corrected heteroscedasticity by specifying the 'weights' argument from the nlme package. We selected

Table 1. Parameter summary (effect estimate, standard error and p-value) of the linear mixed effects analyses of spatiotemporal patterns in per-capita rates of herbivore population change. All explanatory variables are standardized. For both predators, the density estimate from the same period and the density estimate with a one year time lag were modeled as alternatives and the one explaining most variation was retained. Lion and wild dog density were combined into a 'predator' density variable and modeled separately, resulting in a model improvement only for nyala and warthog (estimates presented below the main table). The Akaike weight relative to a null model is reported next to each species' name. Significant effects: p<0.05 '*'; <0.01 '**'; <0.001 '***'.

	White rhino 0.80			Buffalo NULL			Zebra 1.00			Wildebeest 1.00		
	Est	SE	p-value	Est	SE	p-value	Est	SE	p-value	Est	SE	p-value
Intercept	0.02	0.01	0.072 .	0.08	0.02	0.001 **	0.09	0.04	0.012 *	0.23	0.08	0.005 **
Wilddog density (same period)												
Wilddog density (1 yr lag)												
Lion density (same period)												
Lion density (1 yr lag)	0.03	0.01	0.023 *				−0.11	0.02	<0.001 ***	−0.22	0.05	<0.001 ***

	Nyala 1.00			Impala 1.00			Warthog 0.93		
	Est	SE	p-value	Est	SE	p-value	Est	SE	p-value
Intercept	0.01	0.01	0.421	0.06	0.02	0.017 *	0.05	0.03	0.040 *
Wilddog density (same period)									
Wilddog density (1 yr lag)	−0.03	0.01	<0.001 ***				−0.02	0.01	0.006 **
Lion density (same period)									
Lion density (1 yr lag)				−0.09	0.02	<0.001 ***			
Intercept	0.02	0.01	0.145				0.05	0.02	0.040 *
Predator density (same period)	−0.04	0.01	<0.001 ***				−0.03	0.01	0.004 **

Full model structure: per capita rate of population change ~ average rainfall + woody cover + rate of woody thickening + lion density + wild dog density.
Follow-up model structure: per capita rate of population change ~ average rainfall + woody cover + rate of woody thickening + pedator density.

the BAM through step-wise deletion of nonsignificant terms from a full model, evaluating the validity of each deletion using AICc.

Data deposition

Results

Prior to predator population recovery, warthog and impala populations were increasing across sections, the white rhino population was decreasing slightly and the remaining species showed no consistent trend i.e. increasing in some sections while decreasing in others (Fig. 2). However, once predator populations began to recover, populations of species smaller
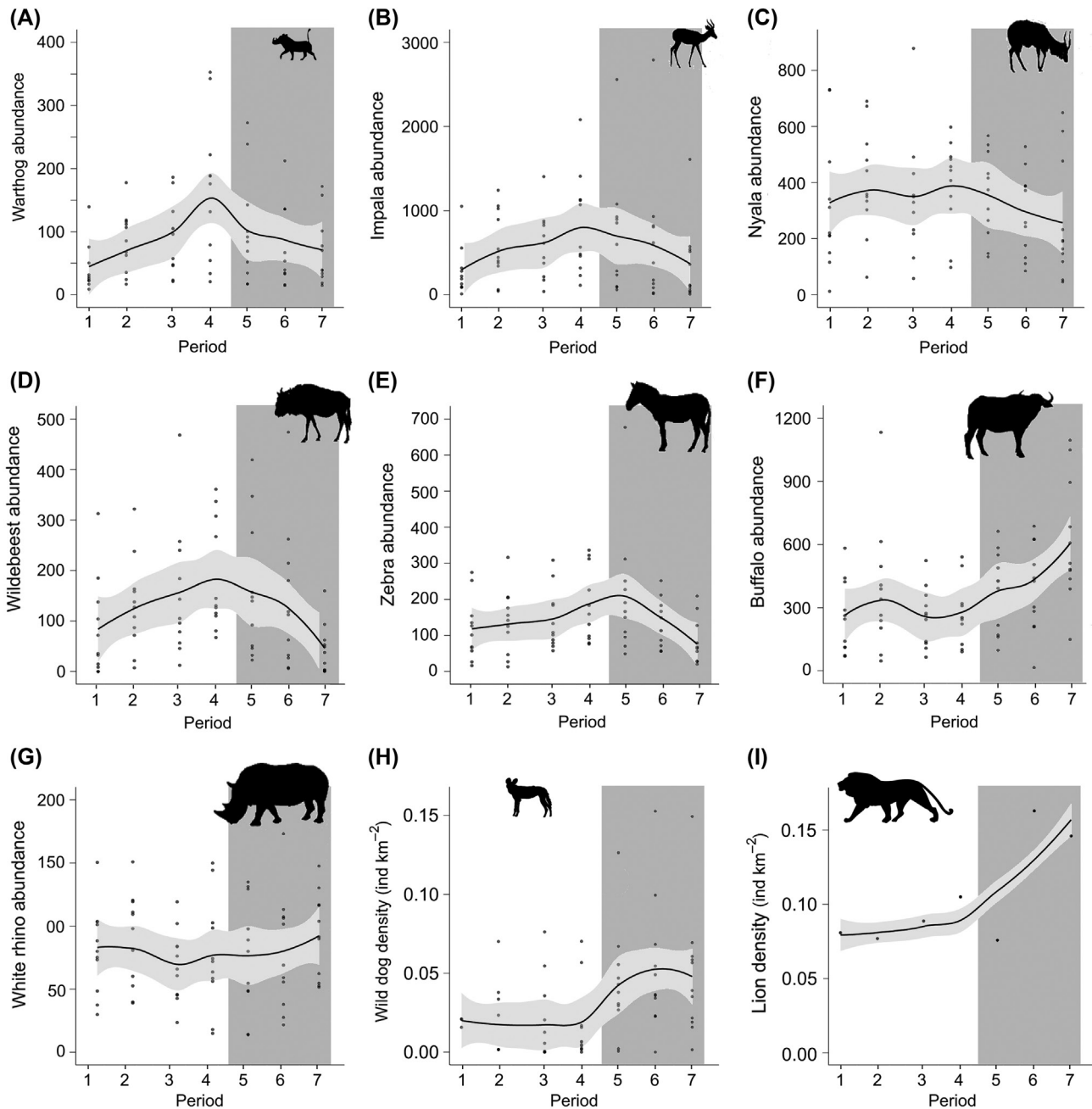
Figure 2. Trends in prey species population abundance (A–G) and predator species population density (H–I) between period 1–7 (1986–2014) in Hluhluwe-iMfolozi Park. Each datapoint indicates a section-specific estimate. The trendlines were obtained using geom_smooth to overlay the line of best fit using a loess smoother (Wickham 2016). The dark grey background shading denotes the period of predator population recovery. Artwork from Phylopic.org.

than buffalo all began to decline (Fig. 2), while buffalo and white rhino populations increased or remained relatively stable.

The rate of population change of zebra, wildebeest, nyala, impala and warthog decreased under conditions of higher predator density (Table 1). Of these five species, only warthog and nyala growth rates responded to wild dog density, with warthog growth rates more closely following wild dog density of the same period, while nyala growth rates more closely followed wild dog density with a one year lag. Despite low VIF values (< 1.1), parameter estimates linking per-capita rate of population change in warthog to either lion or wild dog density were unstable and while warthog populations responded more strongly to wild dog density, single term models indicated a relationship between warthog population change and lion density as well. Combining lion and wild dog density into a single predator density variable improved model fit (Table 1) and thus suggested that both predator densities influenced warthog populations. Declines in nyala population growth rates were equally closely linked to increases in lion numbers and wild dog numbers, and the model was again improved by the combination of the two predators into a single predator density variable.

Variation in the rate of change of impala, wildebeest and zebra populations correlated to changes in lion populations only, with the larger of the three (wildebeest and zebra) responding to the lagged lion density and showing a considerably stronger decline in proportional growth rate to increases in lion density, compared to the smaller species. The two largest species, buffalo and white rhino, showed contrasting responses to changes in predator numbers. None of the predation risk variables were sufficient to explain variation in buffalo abundance, with the null model retained as the BAM. On the other hand, white rhino numbers increased significantly as lion numbers increased.

Rainfall and terrain visibility as measured through woody cover and positive topographic openness were not retained in any of the models, and thus did not influence changes in herbivore abundance. Similarly, the rate of woody thickening within a section also did not explain any variation in herbivore abundance.

The declines in population abundance of smaller species (zebra and smaller) and the increases in population abundance of large species (buffalo and white rhino) ensured that the average biomass of the herbivore community (made up of these 7 species included in this analysis) as a whole tended to increase with increasing predator density (Fig. 3). At higher predator abundance, the herbivore community consisted of proportionally more large species. Within the subset community included in the analysis (white rhino, buffalo, zebra, wildebeest, nyala, impala and warthog), buffalo and white rhino biomass increased in contribution from 74% in period 1–87% in period 7.

Discussion

Our results show top–down population limitation for small to intermediate sized African ungulate species. Only some of the small species (warthog and nyala) were limited by wild dog density, while all small to intermediate sized prey species were limited by lion density. The extent of population limitation was greatest in the prey species preferred by lion (zebra and wildebeest; Clements et al. 2014). We found that predation altered the size structure of the herbivore community, gradually leading to a community made up of larger species.

Discussions of what determines prey vulnerability have centred around two premises of predator diet strategies. Larger-bodied predator species can either target larger-bodied prey (size-partitioning strategy) or they can increase the diversity of the species that they predate upon (size-nested strategy) (Radloff and Du Toit 2004, Hayward and Kerley 2005, Owen-Smith and Mills 2008a). If large predators consume a broader range of prey sizes, prey vulnerability would increase as size decrease, as smaller predators also prey on them. Our study provides evidence that both size-nested and size-partitioning predation occurs. Although impala,
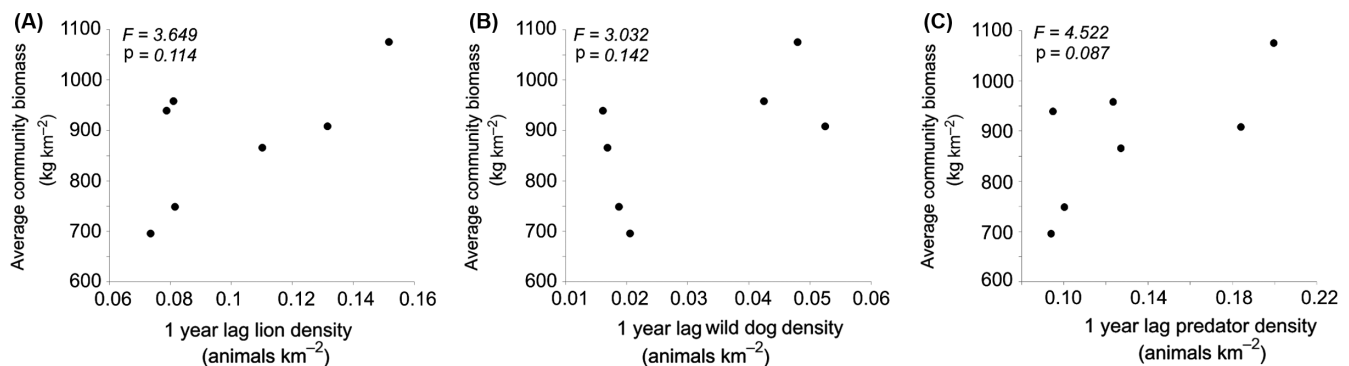

Figure 3. Average community biomass in kg km^{-2} (including white rhino, buffalo, zebra, wildebeest, nyala, impala and warthog) plotted against (A) the one year lagged, averaged annual lion densities per period, (B) the one year lagged, average annual wild dog densities per period and (C) the combined lion and wild dog densities per period (see Methods). The F-statistic and p-value of a linear model are reported in italics in the upper left corner of each panel.

warthog and nyala fall below the preferred prey size range of lion (yet within the accepted range i.e. eaten in proportion to availability; Clements et al. 2014), populations of prey from the size of impala to zebra (average female body mass: 48–310 kg) were all limited by lion density, lending support to the size-nested hypothesis. However, the per-capita reduction in growth rate was most severe for the species within the preferred prey size range of lion, suggesting that the top–down pressure on wildebeest and zebra are more likely to influence population level productivity, despite their larger size. Sinclair et al. (2003) suggest that above a body size threshold of 150 kg, population limitation switches from top–down to bottom–up control. However, in the HiP system, zebra and wildebeest populations (species considerably larger than 150 kg) remained top–down limited.

Surprisingly, predator kill records from HiP reported between 1983 and 2010 showed that buffalo was the species most frequently killed by lion and comprised more than 25% of lion diet. However, regardless of the number of animals consumed, whether predation limits prey population size depends on whether mortality is compensatory or additive. For example, buffalo is a dangerous prey species that are adapted to defend themselves and may even kill lions in the process (Estes 1991, Tambling et al. 2012). This risk is illustrated considering that buffalo kills are made significantly more frequently by male lions than the considerably smaller lioness (Funston et al. 1998). Perhaps in response to this risk, lions preferentially kill old or weakened individuals from bachelor herds (Estes 1991). Thus, if lions are removing individuals already predisposed to die (or at least no longer contributing to population growth) lion predation on buffalo may be compensatory in nature, i.e. predation on post-reproductive individuals where an increase in predation rate has little effect on the productivity of the prey population. In contrast, when hunting smaller species that pose much less risk, lions may be removing healthy individuals with high reproductive potential, that may have still contributed to population growth. In such cases predation related mortality would add to the 'chronic' mortality rate leading prey population mortality rates to correlate positively with increasing predation rates and the population to become top–down limited.

Surprisingly, populations of the largest species did not merely remain unresponsive to predator increases, as one would expect under compensatory predation, but instead increased during the period of predator population recovery. These increases were unrelated to changes in rainfall and, as in the case of rhino populations, correlated directly with the increase in the lion population. One may speculate that such increases could be realized if compensatory mortality frees the remaining animals from intraspecific competition, and thereby promote the survival of the remainder of the population. Alternatively, interspecific competitive release could also play a role, where the larger species may be benefiting from the declining numbers of their potential competitors.

Recorded kills from HiP indicate that wild dog diet consist almost exclusively of nyala and impala (59% and 37% respectively; Somers et al. 2017), yet our analysis shows that impala populations are only limited by lion density. Interestingly, impala only began to show up in wild dog diet in recent years. Between 1983 and 1990, impala and nyala were roughly equally available prey, yet no impala kills were recorded and wild dog diet consisted almost entirely of nyala (Somers et al. 2017). Between 1991 and 2000 impala comprised only 20% of wild dog diet, despite representing roughly 70% of available prey, while nyala declined to approximately 30% of available prey, yet still made up 80% of wild dog diet. In the most recent period (2001–2010) wild dog diet consisted almost equally of nyala and impala, yet nyala have declined to just over 20% of available prey and impala represented almost 80% (Somers et al. 2017). Such shifts in predator diet following reductions in preferred prey are not uncommon (Garrott et al. 2007, Owen-Smith and Mills 2008b). However, this delay in wild dog predation pressure, coupled with the earlier recovery of lion populations and the consistently higher lion numbers, may explain why impala population limitation is linked more closely to lion density than to wild dog.

In HiP, herbivore populations are routinely harvested by park management for sales or relocation to other reserves. These removals have not been spatially uniform and may have disrupted intrinsic population trends and would be interfering with our ability to predict natural drivers of population limitation. Unfortunately, the exact locations of removals are only known for the most recent removals, and historic data were difficult to obtain and spatially inaccurate. However, only removals of buffalo and white rhino exceeded 3% of the population as an annual average (Supplementary material Appendix 1 Table A1). For white rhino, average annual removal over the study period had been 3.8% of the park population, with annual removals exceeding 5% on 5 occasions with a maximum of 10.5% (Supplementary material Appendix 1 Table A1). For buffalo, annual removals exceeded 5% on seven occasions (maximum of 14.3%), for nyala on two occasions (maximum of 11.1%) and impala on two occasions (maximum of 5.8%). Compared to that of rhino and buffalo, removals of smaller species were more spread out across the park (personal communication with park management). Regardless, if management had removed more animals from more open habitat types (for reasons of visibility or accessibility), these artificial removals may explain why we found no significant trends between species abundances and woody cover/topography. Unfortunately, our available data do not allow for further exploration of the influence of management removals.

The unquantified effects of management removals are unlikely to alter our conclusions about species responses to changes in predator numbers since there were no significant correlations between lion density and the proportion of prey animals removed by management. In addition, removal rates of the smaller species (whose populations were found to be

predator limited) were not biased towards pre- or post-predator recovery periods (Supplementary material Appendix 1 Table A1). Moreover, the two species with the highest harvest rates (buffalo and white rhino), maintained positive population growth throughout the predator recovery period.

The link between the visibility of the habitat (woody cover/topography) and predation risk has been well established, particularly for ambush predators such as lion (Elliott et al. 1977, Davies et al. 2016). Yet we did not find that prey species declined faster in dense vegetation of low visibility or in sections that experienced higher rates of woody thickening. With Hluhluwe-iMfolozi being a mesic savanna, woody cover is generally high and thus it is possible that prey's selection for open, more visible areas may occur at finer scale than what our study tested.

Changes in prey population density may have been brought about either by direct mortality or by animals moving between sections. Our estimate of herbivore population change did not differentiate between behavioral responses (migrating out of unsuitable area) or survival responses (numerical changes driven by predation). Either way, predator-induced changes in distribution to less favorable habitat, may also lead to lower survival rates, manifesting in population limitation.

Regardless of the direct mechanism, the protection of predators and their subsequent population recovery altered the population dynamics of small to intermediate sized species gradually shifting the herbivore community assemblage towards larger body size. Such transformations in community structure has also been reported elsewhere, where areas with the greatest predation pressure were dominated by megaherbivores and buffalo (Fritz 1997). The transition to proportionally larger-bodied assemblages may have far-reaching repercussions for ecosystem processes, especially when the shift is towards larger-bodied species and keystone megaherbivores with the potential to bring about major transformation in vegetation structure (Owen-Smith 1988).

Once predators initiate a shift towards larger body size, the process may become self-reinforcing with interspecific competition with a growing contingent of large and megaherbivores placing added pressure on population growth of smaller species. Fritz et al. (2002) demonstrated a negative impact of megaherbivore densities on meso-browser and meso-mixed feeder densities across 31 ecosystems in southern and eastern Africa, citing interspecific competition and/or vegetation structure changes that may be unfavorable to these smaller guilds. Thus top–down population limitation may be a key trigger that drives herbivore communities to become dominated by megaherbivores, an effect perhaps exacerbated in small, fenced reserves where the impact of larger species may be more confined. While recent studies have indicated that we should be particularly concerned about population declines in large herbivore species (> 100 kg, Ripple et al. 2015), our results suggest that small to intermediate-sized species may be particularly vulnerable (see also Owen-Smith et al. 2017),

especially in situations where large carnivores are present in small to medium-sized protected areas.

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