

Contrasting impacts of an alien invasive shrub on mammalian savanna herbivores revealed on a landscape scale

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Abstract

Aim: Habitat loss and fragmentation is one of the main drivers of defaunation, that is the loss of large mammals. Biological invasions could be drivers of such phenomenon. However, their impact on large herbivore communities has not been studied to our knowledge. We made use of a landscape-scale control programme of one of the world's worst invaders, the shrub *Chromolaena odorata*, as a natural experiment to assess how this alien invader affects habitat use by 14 species of ungulates in an African savanna.

Location: Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa.

Methods: At the height of the invasion in 2004, a large-scale control programme was initiated that successfully reduced densities of *C. odorata* across the park. We estimated mammalian herbivore habitat and patch use by dung counts and the presence and density of *C. odorata* along 24 line transects with a total length of 190 km during the peak of the invasion (2004) and a decade after the initiation of a successful control programme (2014). To account for differences in herbivore assemblages between habitats and the preferential invasion of closed savanna woodlands, we analysed the recolonization of previously invaded patches by herbivores based on the change in dung abundance.

Results: Herbivore species differed in how they responded to invaded patches of this non-native shrub. Grazers were the most negatively affected, especially those that avoid predators by running. Browsers were negatively impacted only at the highest invasive shrub densities. Some species, especially bushpig, positively selected invaded patches.

Main conclusions: Large herbivores varied in their response to invasion with differences in impact depending on feeding strategy and predator avoidance strategy, but the majority of ungulates responded positively to the removal of this invasive shrub.

KEYWORDS

Chromolaena odorata, habitat selection, Invasive species, large herbivores, savanna

1 | INTRODUCTION

Mammalian herbivores are major drivers of ecosystem structure and functioning (Estes et al., 2011; Malhi et al., 2016), but the world's

largest herbivores are rapidly being lost (Ripple et al., 2015). In fact, the loss of large fauna may be one of the most underestimated drivers of global change (Dirzo et al., 2014). Ripple et al. (2015) identified land-use change and habitat loss as one of the three major threats to

large herbivore populations. Alien plant invasions are a major cause of habitat loss (Didham, Tylianakis, Hutchison, Ewers, & Gemmill, 2005) and have been linked to the performance of native animals through diverse mechanisms (Levine et al., 2003; Vilà et al., 2011). Alien plants have been shown to affect animal survival rates (Schmidt & Whelan, 1999), feeding habits (Brown, Mitchell, & Graham, 2002) or even life history patterns (Leslie & Spotila, 2001). However, very few studies have looked at the effects of alien plant invasions on native large mammalian herbivore communities (DiTomaso, 2000; Leistriz, Thompson, & Leitch, 1992).

Chromolaena odorata (L.) King and Robinson is listed among the world's worst invaders (Lowe, Browne, Boudjelas, & De Poorter, 2000) and was recently identified as a high-impact invader (Gaertner et al., 2014), because it can drive changes in structure and composition at the ecosystem scale. As such, its invasion is of global concern. *Chromolaena odorata* is a 1.5 to 2 m high shrub, reaching up to 6 m high as a scrambler on trees, and forming dense impenetrable stands (Goodall & Erasmus, 1996; Te Beest, Esler, & Richardson, 2015). Native to South and Central America, it has invaded most of the Paleotropics (Kriticos, Yonow, & McFadyen, 2005; McFadyen & Skarratt, 1996; Raimundo, Fonseca, Schachetti-Pereira, Townsend Peterson, & Lewinsohn, 2007), including southern African and south-east Asian savannas. Recently, it has been recorded in East African savannas (Beale et al., 2013). In these regions, it invades some of the most diverse large mammalian herbivore systems in the world. However, the impact of *C. odorata* on these diverse herbivore communities remains to be assessed. *Chromolaena odorata* could impact large mammalian herbivores in two ways. Firstly, dense stands of the species may affect the native plant community and thus food availability for herbivores. Secondly, *C. odorata* may change predation risk across the landscape (Lauré, Hernández, & Ripple, 2010). Dense patches of *C. odorata* may create ambush opportunities for predators (decreased visibility of escape space for herbivores) or conversely provide shelter for prey utilizing a hiding strategy (see Hugie, 2003; Lima & Dill, 1990). We thus predict that *C. odorata* affects large herbivore species differently, depending on their food preferences and antipredator strategy.

Savanna ungulates can be broadly divided according to their food habits into grazers that feed mainly on graminoids, browsers that feed mainly on herbs and woody species, and mixed feeders that can feed on both (Hofmann & Stewart, 1972). *Chromolaena odorata* has been shown to strongly affect the grass and herbaceous layer. At one site, denser *C. odorata* stands reduced the species richness of grasses and herbs, but not of native woody species (Smith, 2010). At a different site, grass biomass was strongly reduced underneath *C. odorata* shrubs as compared with native shrubs (Te Beest, Esler, & Richardson, 2015). Therefore, we predict that grazers should avoid invaded patches more than browsers and mixed feeders. Besides feeding type, savanna ungulates also span a wide gradient in body mass, from a blue duiker (few kilograms) (*Philantomba [Cephalophus] monticola*) to an elephant (*Loxodonta africana*). The largest of these ungulates are predicted to be relatively insensitive to predation (Owen-Smith, 1988), so *C. odorata* should have the strongest

effects on the predation risk of the smaller to medium-sized species. Conversely, among these smaller ungulates, some may seek out invaded patches to hide from predation, while others may avoid those patches as risky habitat.

We studied the impact of the invasion by *C. odorata* on habitat selection and space use of large mammalian herbivores using a unique park-scale experiment in the savannas of Hluhluwe-iMfolozi Park, South Africa. This park suffered a heavy invasion by *C. odorata* during the 1990s and early 2000s (Te Beest, Cromsigt, Ngobese, & Olf, 2012). At the height of the invasion, 20% of the northern half of the park (Hluhluwe) was covered in dense *C. odorata* monocultures, especially along rivers, forests margins and as an understorey in woodlands (Te Beest et al., 2012). In 2004, Ezemvelo KZN Wildlife (EKZNW—the park's management authority) began a large-scale clearing programme in collaboration with the provincial government (Te Beest, Howison, et al., 2017; Dew, Rozen-Rechels, le Roux, Cromsigt & te Beest 2017), which reduced densities of *C. odorata* with success (currently <5% total park cover). Maintenance of the cleared areas is ongoing. We collected fine-scale (5 meters) data on large herbivore distribution patterns and *C. odorata* density along a park-wide transect network at the height of the invasion in 2004 and after the reduction of *C. odorata* densities in 2014. Linking this ungulate distribution data to spatially explicit data on *C. odorata* density, we looked at potential shifts in habitat selection and space use by herbivores in response to changes in *C. odorata* densities following the large-scale control programme.

2 | METHODS

2.1 | Study area

Hluhluwe-iMfolozi Park (HiP) is a ~ 900 km² fenced reserve located in the KwaZulu-Natal Province, in north-eastern South Africa (see Cromsigt, Archibald, & Owen-Smith, 2017 for detailed description). The area is part of the southern African savanna biome with habitats ranging from open grasslands to closed savanna woodlands, with patches of coastal scarp forest along the north-eastern boundary. The climate is coastally modified, and mean annual rainfall ranges from 550 to 700 mm in the low-lying southern iMfolozi part of the reserve to 700–1000 mm in the hilly northern Hluhluwe part (Balfour & Howison, 2002). Rain falls mostly in a distinct wet season, which occurs in the summer months between November and March. HiP hosts a near-complete set of native ungulates and carnivores (Le Roux et al., 2017; Somers et al., 2017).

2.2 | Study species

Chromolaena odorata was first recorded in South Africa near Durban at the end of the 1940s and reached HiP in 1961 (Macdonald, 1983). *Chromolaena odorata* invades a wide variety of habitats from roadsides and disturbed fields to riverine forests and savannas; however, it is constrained to frost-free habitats (Goodall & Erasmus, 1996). In HiP, the species prefers savanna woodlands and riparian zones (Macdonald & Frame, 1988) and is less likely to invade open savanna grasslands

Species	Feeding type	Body mass ^a (kg)	Dung 2004	Dung 2014
Duiker	Browser	17	50	176
Kudu	Browser	170	144	136
Giraffe	Browser	825	1128	1426
Black Rhino	Browser	925	125	172
Warthog	Grazer	58	1914	379
Waterbuck	Grazer	180	0	10
Wildebeest	Grazer	220	2571	485
Zebra	Grazer	310	2362	406
Buffalo	Grazer	520	6709	4421
White Rhino	Grazer	1600	373	552
Impala	Mixed feeder	44	4360	3039
Nyala	Mixed feeder	63	1269	1332
Elephant	Mixed feeder	2800	2154	2231
Bushpig	Omnivorous	59	1032	450

^aFemale adult body mass from Owen-Smith (1988) except for bushpig (Skinner & Smithers, 1990).

with an undisturbed grass layer (Te Beest, Mpandza, & Olf, 2015). Our assessment of ungulate distribution included 14 large mammalian herbivore species: black rhinoceros (*Diceros bicornis* Linnaeus, 1758), Cape buffalo (*Syncerus caffer* Sparrman, 1779), bushpig (*Potamochoerus larvatus* F. Cuvier, 1822), blue, common and red duiker (*Philantomba [Cephalophus] monticola* Thunberg, 1789; *Sylvicapra grimmia* Linnaeus, 1758; *Cephalophus natalensis* Smith, 1834), African elephant (*Loxodonta africana* Blumenbach, 1797), giraffe (*Giraffa camelopardalis* Linnaeus, 1758), impala (*Aepyceros melampus* Lichtenstein, 1812), greater kudu (*Tragelaphus strepsiceros* Pallas, 1766), nyala (*Tragelaphus angasii* Angas, 1848), warthog (*Phacochoerus africanus* Gmelin, 1788), waterbuck (*Kobus ellipsiprymnus* Smith, 1840), white rhinoceros (*Ceratotherium simum* Burchell, 1817), blue wildebeest (*Connochaetes taurinus* Burchell, 1824) and plains zebra (*Equus quagga* Boddaert, 1785). See Table 1 for more information about the feeding habits and antipredator behaviour of these species.

2.3 | Data collection

From August to October 2004 (high invader densities) and from October to November 2014 (low invader densities), we mapped *C. odorata* density and ungulate distribution (number of dung pellet groups) along a network of 24 transects that varied between 3.9 and 10.4 km in length (7.9 km on average, Figure 1). These line transects are 2 m wide, permanently marked and cut biennially (removing all understorey vegetation, woody and herbaceous up to about 1.5 m high), as part of the ungulate census of the reserve. The transects are evenly distributed across the reserve (excluding a 274 km² "wilderness" area without roads and tourist activities), covering all vegetation types and topography (see Cromsigt, van Rensburg, Etienne, & Olf, 2009 for details). We estimated *C. odorata* density according to six density classes: 0: no plants visible; 1: few individuals present (1–5% cover); 2: 6–25% cover; 3: 26–50% cover; 4: 51–75% cover; and 5: 76–100% cover. Density

TABLE 1 Ungulate species included in the study along with their feeding type, body mass and the total number of dung pellet groups counted for each species

class 5 represented a dense monoculture where no distinction between individual shrubs could be made. In the other classes, we estimated *C. odorata* densities separately on the left- and right-hand side of transects within 5 m of each transect. In 2004, the *C. odorata* density was estimated at a 50-m resolution along transects and this resolution was brought down to every 5 m in 2014 (mostly because *C. odorata* had become much less common after control activities). To make values comparable between years, we averaged the 2014 density scores for every 50 metres and rounded the decimal value to the superior density class value. For each plot (50 m × 10 m area), for both years, we used the maximum of the left- and right-hand side values in the statistical analyses considering that, due to proximity, the less invaded side of the transect is affected by the invasion in the same way as the most invaded side.

Two trained observers walked transects and counted the number of dung pellet groups for all ungulate species within the 2 m width of the cut transect. As white rhino use territorial dung middens, we counted all white rhino dung middens visible from transects. Even though this method might be biased by a change in visibility among habitats, it is the best way to deal with territorial behaviour in white rhinoceros (Cromsigt et al., 2009). We summed the number of pellet groups per species for every 5 m along transects and recorded the spatial position of these 5 m plots in decimal degrees. Performing the dung counting method during years when transects were cut for the park's ungulate census facilitated easy walking and similarly allowed for high dung pile detection rates across habitats. Moreover, we chose the late dry/early wet season for our sampling to avoid the rapid dung decay rates and dung beetle activity of the wet season. Although rainfall was low during both field seasons (June–October 2004: 120 mm; June–November 2014: 115 mm), differences in dung decay rates between years cannot be completely ruled out. Therefore, in the data analyses, we avoided direct interyear comparisons to limit any potential bias.

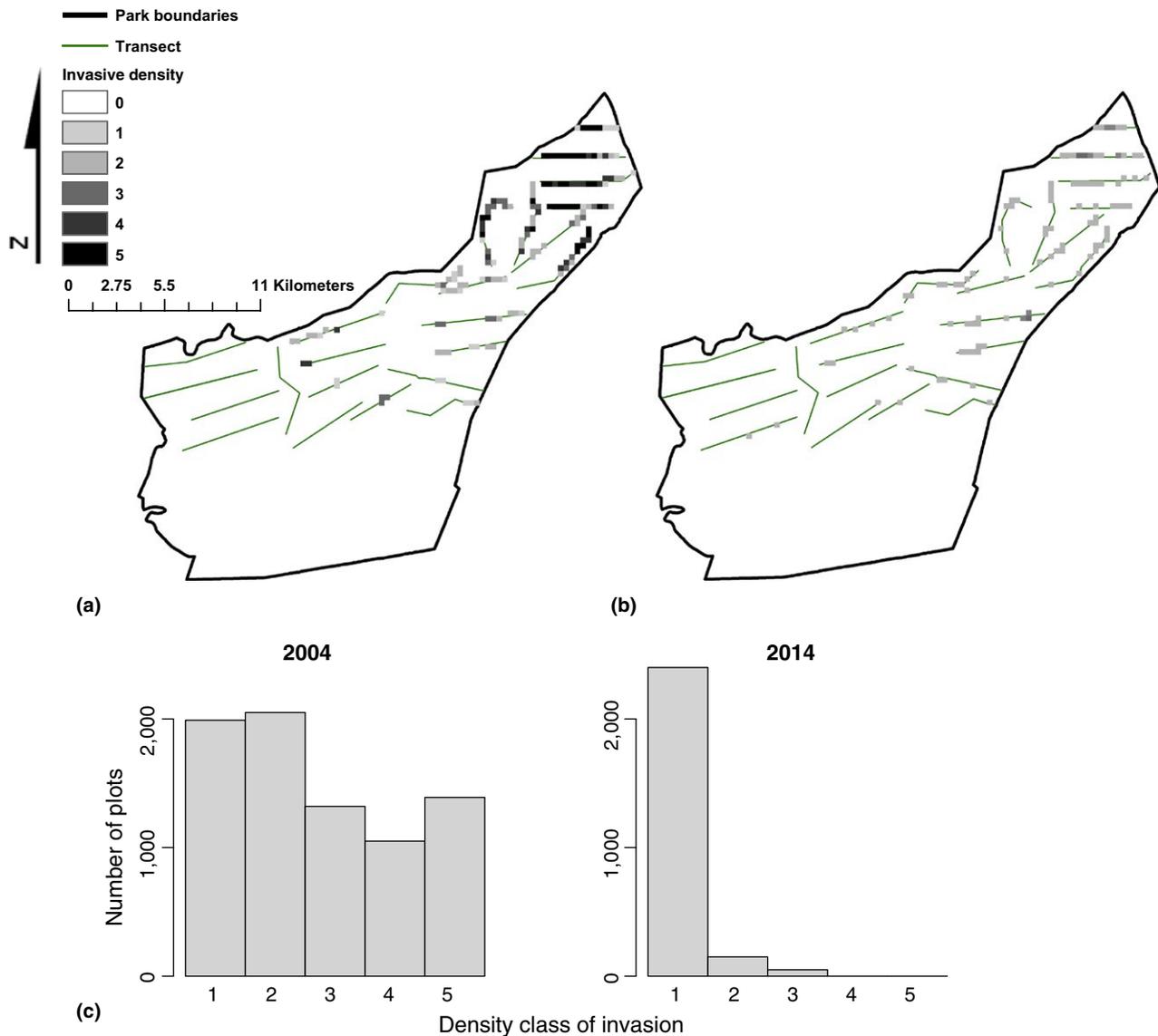


FIGURE 1 Locations of the transects in Hluhluwe-iMfolozi Park (green lines) as well as maximum observed density of *Chromolaena odorata* in a raster layer of 500 × 500 metres pixel width according to five density classes in (a) 2004 and (b) 2014. Density classes are 0 (no *C. odorata* recorded), 1 (1–5% cover), 2 (6–25% cover), 3 (26–50% cover), 4 (51–75% cover) and 5 (76–100% cover). (c) Number of invaded plots for each density class level in 2004 and 2014. [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Data analysis

2.4.1 | Habitat selection

We used a high-resolution remotely sensed (LANDSAT) vegetation map made in 1995 to classify the park into five different habitat types based on woody cover (Meyer, 1999): savanna woodland (dense woody cover), riverine woodland (dense woody cover along rivers), grassland (little or no woody cover), open savanna (grassland with scattered trees) and “other” (reeds, water, soil and sand). Unfortunately, we did not have access to a more recent vegetation map, but the broad habitat categories of this map were consistent with our observations over the decade of our study.

To link ungulate distribution to habitat types and *C. odorata* density classes, we did a two-step habitat selection analysis. As we

only had a complete range of invasion densities (classes 0 through 5) in 2004 when the invasion was at its height, we restricted this analysis to 2004 only. In step 1 we used a descriptive multivariate approach (the Outlying Mean Index OMI approach, Dolédec, Chessel, & Gimaret-Carpentier, 2000) to identify significant associations between species distributions and habitat variables. This analysis is essential to highlight different habitat types and invasion combinations in order to assess for habitat selection bias in the analyses to follow. The OMI analysis gives equal weight to each location (here the set of all 5 × 2 m plots) to describe the habitat and does not take into account the extent to which each plot was used. Its main output is a principal component analysis (PCA) where the axes explain variation in habitat types and invasion density in the study area and the different ungulate species are placed along those different axes. According to the observed correlations between habitat

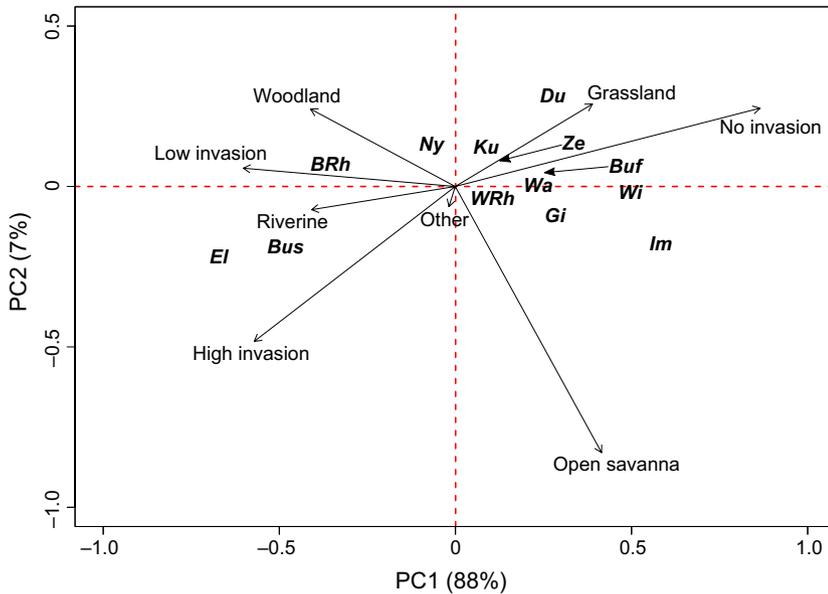


FIGURE 2 Score of each habitat variable to each axis from the OMI analysis. The value in parenthesis in the axis label indicates the deviance explained by the axis. The score of each species is plotted in bold and italic. BRh: black rhinoceros; Bu: buffalo; Bus: bushpig; Du: duiker; El: elephant; Gi: giraffe; Im: impala; Ku: kudu; Ny: nyala; Wa: warthog; Wi: wildebeest; WRh: white rhinoceros; Ze: zebra. The position of buffalo and zebra is indicated with arrows. [Colour figure can be viewed at wileyonlinelibrary.com]

variables, invasion density and ungulate species, a simpler habitat characterization is then extracted (see Figure 2). We computed a canonical OMI analysis to reduce effects of correlation among habitat variables (see Darmon et al., 2012). For the OMI analysis, we combined the *C. odorata* density classes into three broader categories: no invasion (density class 0), low to medium invasion (density classes 1 to 3, 1–50% cover) and high invasion (density classes 4 and 5, >50% cover). This analysis was conducted using the R “adehabitatHS” package (Calenge, 2006).

Subsequently, we performed more detailed resource selection functions (RSFs) for the ungulate species for which the OMI analysis indicated that their distribution was associated with *C. odorata* density levels. RSFs estimate the probability of use of a resource unit by an animal (Boyce & McDonald, 1999; Manly, 2002) by comparing “used resource units” (units where a certain species was found) with an equal number of randomly available units. In our case, “used units” were the 5 × 2 m plots containing dung of a certain species. For each species except duiker, we randomly picked an equal number of 5 × 2 m plots where no dung of that species was found. We did not include duiker in the analysis because the sample size was too low to run the models. Random plots were only selected from transects that occurred within the same management section of the park as the “used units.” The park is divided into five management sections that were created according to the diversity and history of the park (Te Beest, Owen-Smith, Porter, & Feely, 2017). We followed this approach to limit the randomly available locations to an area that was reasonably accessible from the used locations. We then estimated habitat selection as logistic regressions on the binomial response (used vs available habitat) for each species and for each year. As predictors of habitat selection, we used the six density levels of *C. odorata* and the habitat combinations that were highlighted with the OMI analysis as fixed effects. We used the *anova* function of the package “car” in R (Fox & Weisberg, 2011) to determine whether the *C. odorata* density significantly affected a species’ habitat selection. We also computed RSFs without the *C. odorata* densities. For every model,

we performed a *k*-cross-validation for every observation. We calculated the weighted rate of error (WRE) and compared it for the models with or without *C. odorata* densities. For those ungulate species where the WRE and/or chi-square deviance tests (*anova* function in R) showed a significant improvement in model fit when taking *C. odorata* densities into account, we calculated the logarithm of the odds ratios (see Figure 4) as a measure of selection (positive values indicate selection).

2.4.2 | Recolonization analysis

Because the invasion of *C. odorata* is habitat-specific, the selection of herbivore species for or against invaded patches could be confounded by their habitat selection independent of *C. odorata* invasion. Therefore, we did an additional analysis where we controlled for habitat type and looked at shifts in use of the same areas between 2004 and 2014. We limited this analysis to species whose habitat selection was shown to be affected by the invasion in the RSFs. We tested whether a decline in *C. odorata* density between 2004 and 2014 in a particular area was associated with an increase (recolonization) or a decline (abandonment) in dung abundance in that area. As densities of *C. odorata* in 2014 were very low compared to 2004 (see Figure 1) and there were no observations of density classes 4 and 5 in 2014, we assumed that *C. odorata* densities in 2014 were negligible compared to 2004. We merged adjacent 50 m plots in the 2004 data set with the same invasion density value into zones using the same three broader invasion density classes that were used in the OMI analysis: “highly invaded in 2004 (density class 4–5, >50% cover),” “low invasion in 2004 (density class 1 to 3, 1–50% cover),” and “not invaded in 2004 (density class 0)”. We then used the same zones for 2004 and 2014 and, for each zone, calculated the mean change in dung for each species between 2004 and 2014, which we then related to the change in invasion density between these two years. We used generalized least squares models (using the “nlme” package in R) to model the changes in dung abundance between 2004 and 2014 using the change in *C. odorata* density as the predictor variable and a matrix of distances

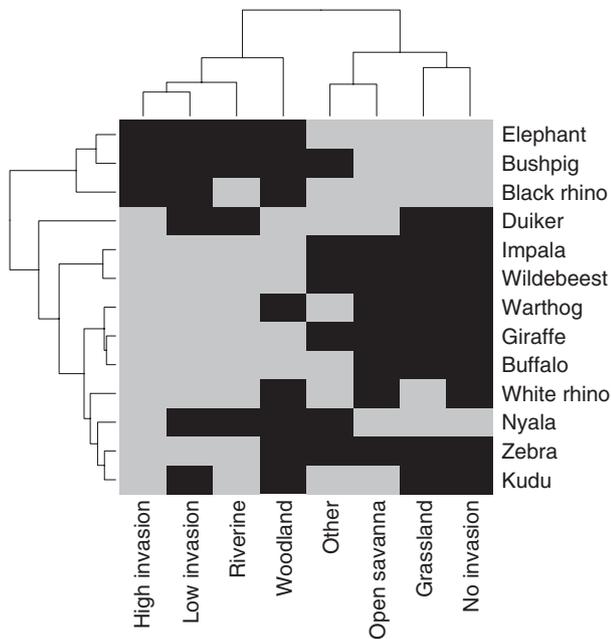


FIGURE 3 Results from the OMI analysis. The matrix of squares shows whether or not each ungulate species selected for a certain habitat type or invasion density. *Chromolaena odorata* density is given according to three levels: high (>50% cover of *C. odorata*), low (1–50% cover) and no invasion. A black square at the intersection of a species and a habitat indicates positive selection, while grey indicates no significant selection. The tree above the matrix shows the correlation structure among habitats, including the association of habitats with different levels of *C. odorata* invasion. The correlation structure tree on the left-hand side of the matrix shows the (dis) similarity in habitat selection among ungulate species. [Colour figure can be viewed at wileyonlinelibrary.com]

among zones as an autocorrelation structure. This matrix included the Euclidean distances for each pair of zones using the coordinates of the centre of each zone. For this analysis, we only used the data of the eight most northerly transects that were most densely invaded in 2004 so as to limit our analyses to the most invaded zones. For the interpretation

TABLE 2 Results of the RSF analyses. For each species, we give the difference in the weighted rate of error (Δ WRE) between models with and without *Chromolaena odorata* density as predictor. In addition, we give the deviance difference and *p*-value (*anova* function) of the comparison between these two models. In bold we highlighted the species that were significantly affected in their habitat selection by the invasion of *C. odorata* ($p \leq .05$)

Species	Δ WRE*1000	Deviance difference	Chi-square test <i>p</i> -value
Black Rhino	4	-16	.1
Buffalo	-1.9	-129	<.001
Bushpig	-4.7	-59	<.001
Elephant	-2	-56	<.001
Giraffe	0.6	-19	.048
Impala	-0.9	-57	<.001
Kudu	14	-7	.6
Nyala	-1.3	-33	<.001
Warthog	-1	-37	<.001
Wildebeest	-2	-68	<.001
White Rhino	1.6	-18	.03
Zebra	-0.4	-27	.002

of results, we only considered models that were significantly different ($\alpha \leq 0.05$) from the null model (using the *anova* function).

3 | RESULTS

3.1 | *Chromolaena odorata* distribution and dung counts in 2014 vs. 2004

In both 2004 and 2014, the invasion of *C. odorata* was concentrated in the north with pockets of invasion in the central part of the park (Figure 1). Although the full spatial extent of the invasion was fairly similar for both years, invasion density was lower in almost all (97%) of the invaded plots in 2014 compared to 2004. Moreover, the number of plots invaded by *C. odorata* was much lower in 2014 than 2004 (Figure 1c) and, whereas high-density plots (class 4 or 5) were common in 2004, they had become absent by 2014 (Figure 1c).

The total number of dung pellet groups counted was much lower in 2014 than in 2004 for all grazer species, except white rhino (Table 1). This number was fairly similar for browsers, mixed feeders and omnivores, reflecting a general decline in ungulate numbers in HiP (Le Roux et al., 2017). We counted very few waterbuck and this species was, therefore, not included in further analyses.

3.2 | OMI analysis

The invasion of *C. odorata* was more strongly associated with closed habitats (riverine vegetation and savanna woodland) than with open habitats (open savanna and grassland), see Figure 2. The first two axes of the PCA explained a high percentage of the variation in habitat combinations (27% and 21%, respectively) where the first axis differentiated non-invaded (and open) and invaded (and closed) habitats and the second axis grasslands and savanna woodlands (see contributions of each habitat descriptor to each axis of the PCA in Table S1). Moreover, this first axis of the OMI analysis explained 88% of the variation in habitat selection among the ungulate species (the second

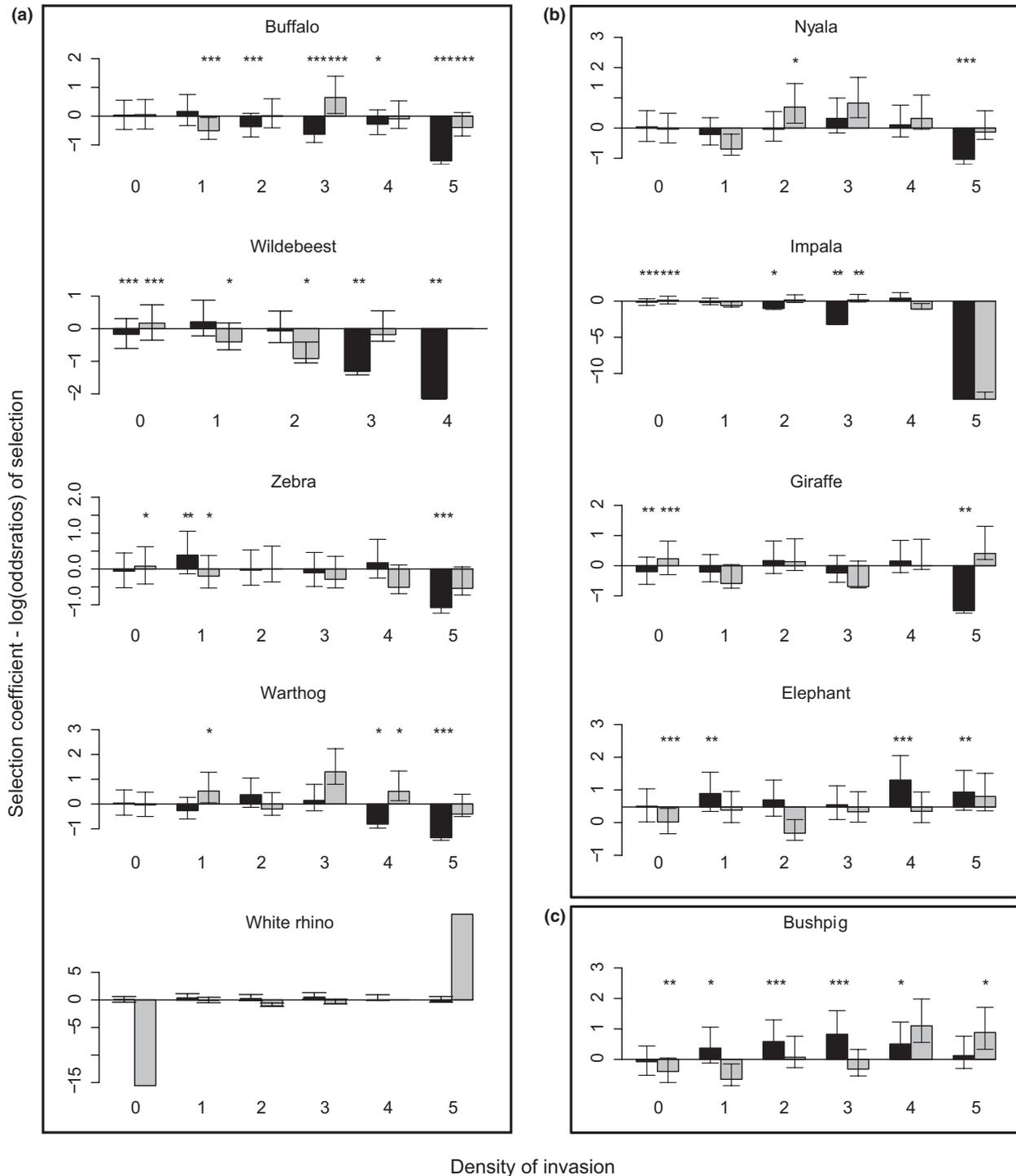


FIGURE 4 Selection coefficients (log(odds ratios)) resulting from the resource selection functions against the level of *Chromolaena odorata* density. Density classes are 0 (no *C. odorata* recorded), 1 (1–5% cover), 2 (6–25% cover), 3 (26–50% cover), 4 (51–75% cover) and 5 (76–100% cover). Positive log(odds ratios) indicate selection for a density level, while negative values indicate avoidance. Black bars are the selection coefficients for closed habitats (savanna woodland and riverine habitat), and grey bars are those for open habitats (grassland and open savanna). Asterisks represent significant deviations from reference (effect when no invasion): * $p < .05$, ** $p < .01$, *** $p < .001$. No bar plotted means that the combination of that particular habitat and that particular invasion density is not present in the data for that particular species (no prediction could therefore be made). (a) Grazers. (b) Mixed feeders and browsers. (c) Omnivores. We only show the ungulate species for which *C. odorata* density significantly contributed to RSFs (see Table 2).

TABLE 3 Results of the recolonization analyses. Zones are clusters of plots adjacent to each other with similar *Chromolaena odorata* densities in 2004 (zone 0 reflects no invasion, zone 1 low invasion density classes 1 to 3 (1–50% cover) and zone 2 high invasion density classes 4 and 5 (>50% cover)). The “zone” variable is considered significant if its *p*-value is <0.05 (highlighted in bold)

Species	Coefficient	DDF	F-value	<i>p</i> -value
Buffalo	Intercept	1	1.56	.21
	Zone	2	3.47	.03
Bushpig	Intercept	1	2.86	.09
	Zone	2	0.66	.52
Elephant	Intercept	1	3.20	.07
	Zone	2	0.17	.85
Giraffe	Intercept	1	0.23	.63
	Zone	2	0.37	.69
Impala	Intercept	1	3.78	.05
	Zone	2	0.01	.98
Nyala	Intercept	1	1.40	.23
	Zone	2	0.41	.66
Warthog	Intercept	1	15.6	.51
	Zone	2	0.66	.001
White Rhino	Intercept	1	1.76	.18
	Zone	2	0.58	.56
Wildebeest	Intercept	1	19.0	<.0001
	Zone	2	6.99	.001
Zebra	Intercept	1	33.2	<.0001
	Zone	2	3.75	.02

axis explained 7.42%), indicating that the separation between invaded (closed) habitats and non-invaded (open) habitats drives differences in habitat selection among species. There were two contrasting patterns of habitat selection (see the correlation tree on the left-hand side in Figure 3). Nyala, duiker, kudu, black rhino, elephant and bushpig selected for closed and/or invaded habitats whereas the other eight herbivore species selected for open and/or non-invaded habitats. Elephant, bushpig and black rhino were the only herbivores not avoiding highly invaded habitats. Other closed-habitat specialists such as kudu, nyala and duiker avoided high-density invaded patches but not the low-density invaded patches.

3.3 | Resource selection functions

Taking the results of the OMI analysis into account, we simplified the habitat predictor from 5 to 2 levels: open (grassland, open savanna and other) vs. closed habitat (savanna woodland and riverine). Adding *C. odorata* density as predictor significantly improved the fit of the RSFs for 10 of the 12 ungulate species that we included (Table 2). For black rhino and kudu, *C. odorata* density did not significantly explain variation in their habitat selection. For the remaining 10 species, we observed two contrasting patterns: species that selected

for invaded patches and species that avoided them (Figure 4). We considered white rhinos and giraffes even though their RSFs showed a positive variation in WRE with k-cross-validation to confirm the absence of results. Elephant and bushpig selected for highly invaded and medium-invaded patches, respectively. Seven species avoided invaded patches. Buffalo, wildebeest and warthog avoided patches with *C. odorata* cover >50%, while nyala, giraffe and zebra only avoided the most highly invaded patches (cover >75%). Impala avoided the low- to medium-invaded patches (6–50% cover), but we did not observe significant effects for the more highly invaded patches (> 50% cover), probably due to low occurrences. We found no significant selection or avoidance effects of *C. odorata* invasion on white rhino. All significant avoidance effects of the *C. odorata* invasion were found in closed habitats (Figure 4, black bars).

3.4 | Recolonization analysis

Of the 10 species for which RSFs indicated that *C. odorata* density negatively explained habitat selection, four also turned out significant in the recolonization analysis: buffalo, wildebeest, zebra and warthog (Table 3). For the first three species, the relative increase in amount of dung from 2004 to 2014 was stronger in zones that were heavily invaded in 2004 than in the less heavily or not invaded zones (Figure 5). For buffalo and wildebeest, this was expressed as an actual increase of amount of dung in 2014 in previously heavily invaded zones, whereas for zebra, it was expressed as a less dramatic decline in these zones (Figure 5). We found no significant difference in recolonization for warthog.

4 | DISCUSSION

At Hluhluwe-iMfolozi Park, *C. odorata* significantly affected the habitat selection of all species except for black and white rhinos, and kudu. The species that were affected showed diverse responses, with some species avoiding *C. odorata* invaded patches (buffalo, wildebeest, giraffe, zebra and warthog), while others selected these patches (bushpig and elephant) or showed more mixed results (impala and nyala). Moreover, species differed in their response to the extent of invasion. Some responded to relatively low levels of invasion (e.g. wildebeest and buffalo), while others only responded to the most densely invaded patches (e.g. nyala, giraffe, zebra, warthog). As we hypothesized, these different responses among species are consistent, to a large extent, with variation in feeding type and predator avoidance among herbivore species.

We hypothesized that grazers would respond more strongly to invasion by *C. odorata* than browsers, because *C. odorata* most strongly affects the grass layer and transforms grasslands to shrublands (Te Beest, Esler, et al., 2015, Te Beest, Howison, et al., 2017). Our results confirmed this hypothesis. All strict grazers included in our study responded negatively to invaded plots, except white rhino. However, white rhino use middens (territorial dung piles) that are often not directly associated with their foraging patches. This makes

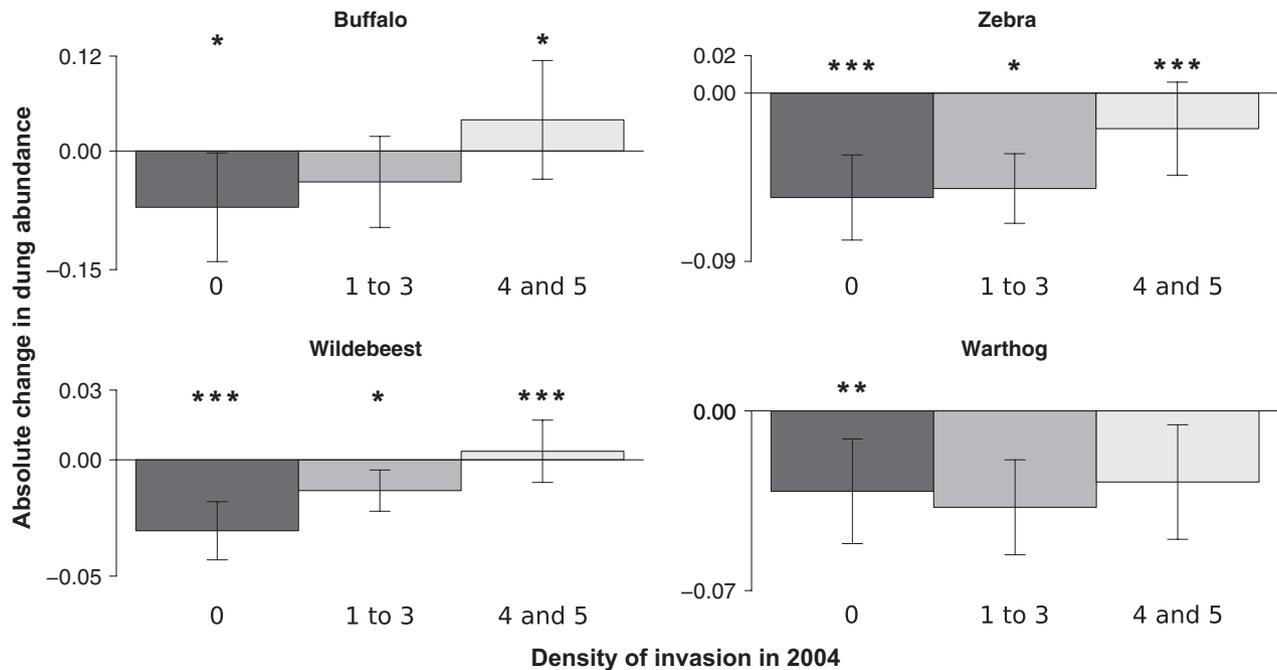


FIGURE 5 Results from the recolonization analyses showing the average absolute change in amount of dung between 2004 and 2014 against *Chromolaena odorata* density class. This reflected a change in amount of dung in clusters (Zones, see methods) with the same *C. odorata* density during 2004. We only show the ungulate species for which *C. odorata* density significantly affected the change in dung amounts (see Table 3). *Chromolaena odorata* density is given according to three levels: high (>50% cover of *C. odorata*), low (1–50% cover) and no invasion. Asterisks represent significant deviations from reference (conditions of no invasion in 2004): * $p < .05$, ** $p < .01$, *** $p < .001$.

it difficult to use dung counts for assessing fine-scale habitat selection by rhino species (Cromsigt et al., 2009). The other grazers in our study frequently defecate where they eat. The strict browsers in our study were less affected by the invasion, with only giraffe avoiding the highest density patches and no significant responses for kudu and black rhino (Table 2). But, similarly to white rhino, dung counts are difficult to use for assessing black rhino habitat selection. The mixed feeders showed a mixed response, where nyala only avoided the highest density plots, while impala avoided medium-invaded plots.

It does not appear that *C. odorata* itself is a food source for ungulates in Hluhluwe-iMfolozi Park. Although goats have been recorded to feed on it (Basha, Scogings, Dziba, & Nsahlai, 2012), during many years of fieldwork in HiP, we rarely observed it being eaten by any of the ungulates, apart from some signs of browsing by elephant and black rhino on twigs and occasional browsing by nyala (Cromsigt and Te Beest, personal observations). However, the selection of invaded patches by bushpig may be indirectly related to food availability because *C. odorata* enhances soil nutrient status (Te Beest, Esler, et al., 2015) which may increase numbers of the soil dwelling insects and larvae that bushpig feed on.

Several of the largest ungulate species did not respond significantly to *C. odorata* invasion (black-and-white rhino) or selected for invaded plots (elephant). This fits with our hypothesis that *C. odorata* may change the predation risk landscape for ungulates. If so, we predicted that the largest species would not respond negatively. At the same time, elephants are the only species that are actually able to walk through dense *C. odorata* monocultures (Te Beest, personal observations) and

the observed selection by elephants can be explained by their major movement routes traversing some of the most heavily invaded savanna woodlands of HiP. Predation risk may also be an additional explanation why grazers responded more strongly than browsers. Dense vegetation increases the perceived risk of herbivores (Laurd re et al., 2010), and mesograzers have been shown to respond more strongly to dense vegetation than mesobrowsers (Le Roux, 2016).

The OMI analysis showed a strong association of *C. odorata* invaded patches with savanna woodland and riverine habitat. As already mentioned in the Methods, this means that the effects of *C. odorata* and habitat type are likely confounded. For example, the fact that most grazers avoided invaded areas may not be due to the invasion but due to them preferring open grass-dominated habitats. However, we controlled for this bias by estimating selection coefficients for *C. odorata* density levels separately for closed and open habitats (Figure 4). This showed that for all grazers, and also the mixed feeders, the extent of avoidance of invaded patches increased with increasing *C. odorata* density within the same habitat. While closed habitat was barely avoided in the absence of or at low density of *C. odorata*, it was strongly avoided at high densities (see Figure 4a and b). This suggests that we are indeed looking at an effect of *C. odorata* on ungulate habitat selection. This conclusion is further supported by the results of the recolonization analyses for buffalo, wildebeest and zebra.

Our results suggest that low-level invasion (<25% cover) only affected habitat selection of the ungulates to a limited extent. In addition, species such as buffalo, wildebeest and zebra, that strongly

avoided patches, that were medium to heavily invaded in 2004, had by 2014 recolonized these areas following clearing of these patches. These results suggest that the focus of clearing programmes should be on the heavily invaded patches (>50% cover) to reduce immediate impacts (Gaertner et al., 2014), while at the same time managing low-density areas to prevent them from becoming dense. This approach has been successfully implemented in HiP in the last ten years, albeit at a high economic cost (Te Beest, Howison, et al., 2017; Dew et al., 2017). Our results show that these clearing programmes have potential to restore animal habitat selection. This is also reflected in previous work by Mgobozi, Somers, and Dippenaar-Schoeman (2008), who showed that clearing allowed native spider communities to be restored.

Our results suggest that in the long run, unmanaged, dense invasions of *C. odorata* lead to strong shifts in habitat selection of several ungulate species, and particularly grazers and smaller species. Ultimately, if non-invaded habitat is limited, this could lead to shifts in the ungulate community towards a browser and intermediate feeder community, and towards a community with reduced numbers of small- to medium-sized ungulates. Our data did not allow us to explore such ungulate community- and population-level consequences of the invasion in Hluhluwe-iMfolozi Park. But we did show that the large-scale clearing programme has led to species restoring their habitat use and this may have come in time to prevent population-level effects on some of the species that responded in terms of habitat selection. This example from Hluhluwe-iMfolozi Park could serve as an example for protected areas elsewhere where the invasion of *C. odorata* or other high-impact invaders, such as *Lantana camara* L. or *Parthenium hysterophorus* L. is in its early stages and/or not currently managed (Beale et al., 2013; Rejmánek, Huntley, Le Roux, & Richardson, 2016).

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AUTHOR CONTRIBUTIONS

JPGMC and MTB conceived the idea and collected the 2004 data. DRR, LAD and ELR collected the 2014 data, with logistic support from DD. DRR analysed the data and wrote the manuscript. All authors contributed to the writing of the manuscript.

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BIOSKETCH

David Rozen-Rechels is doing a PhD thesis at the iEES-Paris about thermal habitat and micro-habitat selection and its implications in the optimization of thermoregulation. He studies the pattern of space use, activity and thermal preferences of the viviparous lizard and the African elephant in interaction with landscape heterogeneity in temperature and water.

SUPPORTING INFORMATION

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