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Effekterna av en invasiv växt på afrikanska stora växtätare

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Abstract

Invasive plants, growing and spreading outside of their native range, can severely modify ecosystems. Herbivory has often been seen as a potential control of invasions, but has rarely been considered as a potential impacted trophic level. Considering the habitat selection by large herbivore being a reflection of their feeding habits and predator avoidance, I studied the impact of the invasive *Chromolaena odorata* on African large herbivores in Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa. This plant is not eaten by the animals but affects the diversity of the grass species, the height and cover of woody species and can create high and thick walls as a barrier for most animals. Abundance of 14 species of herbivores was estimated by dung counting, and the presence and density of the invasive shrub was estimated every 5 meters on 24 transects in the park in 2004 (high density of invasive) and 2014 (low density of invasive). This data was used to understand a predictive habitat selection analysis (Resource Selection Functions) and to analyse the recolonization of previously invaded patches based on the change of dung abundance. A Principal Component Analysis showed that closed woody habitats are the most invaded. The results are a mirror of the high heterogeneity of habitats and herbivores in African savannas. Grazers (buffalo, zebra, warthog, and wildebeest) as well as browsers (nyala) avoided high density patches that are a physical barrier to selection. Grazers seem also to avoid less dense patches where food availability might be diminished and where ambush predators could hide. However, bushpigs select invaded patches, which may be used as a shelter against predators for example. Other species appear to ignore the invasion; because their home area does not overlap the invaded area (impala) or because the invasion does not affect them (elephant).

Introduction

Across recent history, human movements have facilitated the dispersion of plant and animal species to places outside their native range. Some of these alien species can sustain in this new environment (they are *naturalized*) or even spread in it, which means that they are *invasive* (Richardson et al. 2000). They impact the ecosystem by altering the plant community structure, or the structure of the higher levels in the trophic network; they can also affect the ecosystem processes through nutrient cycling (primary and secondary production), change hydrology, and fire regimes (Levine et al. 2003). Many studies have been conducted on the impact of native herbivores on alien plants compared to native plants, especially in the case of insects (e.g. Agrawal and Kotanen 2003, Dietz et al. 2004, Johnson and Cushman 2006, Huang et al. 2010, Krebs et al. 2011). However invasive plants can also have an impact on the higher trophic levels species. Following Levine et al. (2003), exotic plants could change survival rates of animals (e.g. birds nest that are not as well protected as they are in native trees), the animals feeding habits (e.g. pollinators will visit alien plants where nectar is more abundant) or distribution (e.g. worms concentrated around alien plants). Few studies have been published, however on the impact of introduction, naturalization and invasion on herbivores.

The invasion by alien plants could potentially impacts herbivores by bottom-up processes. Most invasions reduce the diversity of primary producers, leading to a modification of the food availability if herbivores don't feed the on alien species (Vilà et al. 2011). The dominance of an invasive species, growing in dense patches, will also create ambush opportunities for a predator, or a shelter for a prey. This is a hypothetical top-down effect of the invasion on herbivores, modifying the "landscape of fear" that describes the modification of the predation risk in the different areas of use of an animal (Laundré et al. 2010). Such modifications could lead to avoidance of previously selected patches by herbivores, or to the inverse effect; i.e., it could change their habitat selection.

Following Johnson (1980), selection is the process by which an animal chooses the concerned object. The animal is selective if the component is used more than expected according to its availability (accessibility). Hall et al. (1997) define the habitat "as the resources and conditions present in an area that produce occupancy-including survival and reproduction-by a given organism". Habitat selection is then the disproportionate use of a combination of environmental parameters (vegetation, water, …) compared to what is available.
Habitat selection is driven by the quality of the food (e.g. Bjørneraas et al. 2012), but also by intraspecific competition (e.g. density, see van Beest et al. 2014), interspecific competition (e.g. Bolesi et al. 2004), predation (e.g. Valeix et al. 2009) and also facilitation (e.g. Wegge et al. 2006) at the food patches scale. At the landscape scale drivers are also water (e.g. Valeix 2011), climate (e.g. Martin 2001)… Any perturbation that could have a slight effect on one or many of these parameters might change the habitat selection behavior.

Invasive plants can cause such perturbation. In this study I look into the impact of the invasion by *Chromolaena odorata* (L.) King and Robinson on large mammalian herbivores in South Africa. *C. odorata* is an Asteraceae, which forms shrubs 1.5 to 2 meters high, but it can reach as high as 3 meters as stand-alone, and 10 meters when climbing trees (Zachariades and Goodall 2002). This shrub can also form dense stands of up to 15 plants per m^2 (Goodall and Erasmus 1996) thereby creating impenetrable walls. *C.* odorata is

originally from South and Central America. It has already invaded India and South-East Asia in the 1870s and then spread to Oceania (McFadyen and Skaratt 1996). Its invasion in South Africa has been first recorded at the end of the 1940s (Goodall and Erasmus 1996). Present on every continent except Europe, this shrub is one of the world's most widespread invaders. C. *odorata* invades habitat from forests to semi-arid savannas; however it is constrained to grow only in frost-free habitat (Goodall and Erasmus 1996). It affects both the diversity of the grass community and the canopy cover and the height of woody species (Smith 2010). However, *C. odorata* is not a superior competitor compared with one of the main savanna grasses, *Panicum maximum*. Its invasive capacity has been said to be due more to its dispersal capacity and its greater light interception (te Beest et al. 2013). It seems that this shrub invades mainly woodland habitats and riparian zones (Macdonald and Frame 1988) and hardly invades grasslands (te Beest et al. 2015).

Very little is known about the impact of the *C. odorata* invasion on native faunal communities. Mgobozi et al. (2008) showed that *C. odorata* invasion reduced the species richness and composition of native spiders. Clearing of the shrub did restore spider communities. However, the responses of much larger fauna remain poorly understood. African ungulates habitat selection might then be affected by the *C. odorata* invasion. The aim of my thesis is to identify how *C. odorata* invasion affects the patterns of habitat selection of savanna large herbivores. Savannas are known to be complex and heterogeneous environments allowing the cohabitation of diverse ungulates (Cromsigt and Olff 2006). Therefore the response of each ungulate species likely differs according to their individual behavior and habits.

Savanna ungulates can be broadly divided according to their food habits. Following Hofmann and Stewart (1972) classification, grazers are herbivores feeding on grasses while browsers feed mainly on foliage. Mixed-feeders feed on both, depending on the area, the season or other biotic or abiotic parameters. I predict that the modification of the grass diversity impact grazers which will avoid invaded areas. Ungulates may also differ in the way they respond to predation risk. All the species studied in my thesis are presented and classified in Table 1.

To study habitat selection/avoidance patterns in response to *C. odorata*, I used the possibility to compare similar habitats in two different states: invaded and non-invaded. Those two treatments are obtained by collecting data in the Hluhluwe-iMfolozi Game Reserve, KwaZulu-Natal, South Africa before and after the start of an intensive clearing program. I am then able to study a potential shift in habitat selection in response to changes in *C. odorata* densities following this clearing program.

I first quantified the distribution of *C. odorata* between a year of high abundance of invading shrub (2004) and a year of low abundance (2014). I also studied what habitats are mainly invaded by the shrub (1).
The second part of my study focused on the predictive habitat selection of the ungulates according to the invasion. I quantified avoidance or selection of patches representing different *C. odorata* density classes for the highly and lowly invaded years (2).
Such obtained patterns could be linked to habitat bias. In other words, an observed selection of invaded patches could be in reality the selection of a habitat more invaded than the others. If the invasion is habitat dependent as (1) might show, some avoidance or selection patterns of invaded patches could only be due to avoidance or selection of the most invaded

habitat. I then studied the potential recolonization or abandonment of patches that were heavily invaded patch in 2004 but not in 2014, assuming that the type of habitat didn't change in 10 years (3).

Species	Food habits (Leuthold 1977)	Type of habitat selection (Observation)	Antipredation behavior** (Leuthold 1977)
African Elephant (*Loxodonta africana*)	Mixed feeder	All	I/A
White Rhino (*Ceratotherium simum*)	Grazer	Grasslands	I/A
Black Rhino (*Diceros bicornis*)	Browser	Woodlands	I/A
African Buffalo (*Syncerus caffer*)	Grazer	Grasslands	A
Plain's Zebra (*Equus quagga*)	Grazer	Grasslands and Open Woodlands	F
Wildebeest (*Connochaetes taurinus*)	Grazer	Grasslands and Open Woodlands	F
Waterbuck (*Kobus ellipsiprymnus*)	Grazer	Grasslands and Open Woodlands	F
Greater Kudu (*Tragelaphus strepsiceros*)	Browser	Woodlands	F
Impala (*Aepyceros melampus*)	Mixed feeder	Grasslands and Open Woodlands	F
Nyala (*Tragelaphus angasii*)	Browser	Woodlands	F
Warthog (*Phacochoerus africanus*)	Grazer	Grasslands	H
Common Duiker (*Sylvicapra grimmia*) and Red Duiker (*Cephalosus natalensis*)	Browser	Mixed	H
Bushpig (*Potamochoerus larvatus*)	Omnivorous*	Woodlands	H
Giraffe (*Giraffa camelopardalis*)	Browser	Mixed	F

Table 1. Food habits, antipredation behavior and body mass in studied ungulates. *: added using Wilson et al. (2009). **: Ignoring (I), Attack (A), Flight (F), Hiding (H).

Methods
The study area
Hluhluwe-iMfolozi Park is an 89,655 ha fenced reserve located in the KwaZulu-Natal province, in South Africa. The area is part of the southern African savanna biome. The habitat is heterogeneous ranging from open grasslands to closed *Acacia nicolata* woodlands (Owen-Smith 2004). This heterogeneity could be explained by the grazer-fire interaction impact (Archibald et al. 2005) and the various environmental conditions met in the park. For example, annual rainfall ranges from 650-700 mm in the southern iMfolozi acacia savanna part of the reserve to 700-1000 mm in the northern Hluhluwe part (Owen-Smith 2004). Rain falls in a distinct wet season, which occurs between October and March. The park is divided into 5 management sections; I only did my sampling in 4 of them.
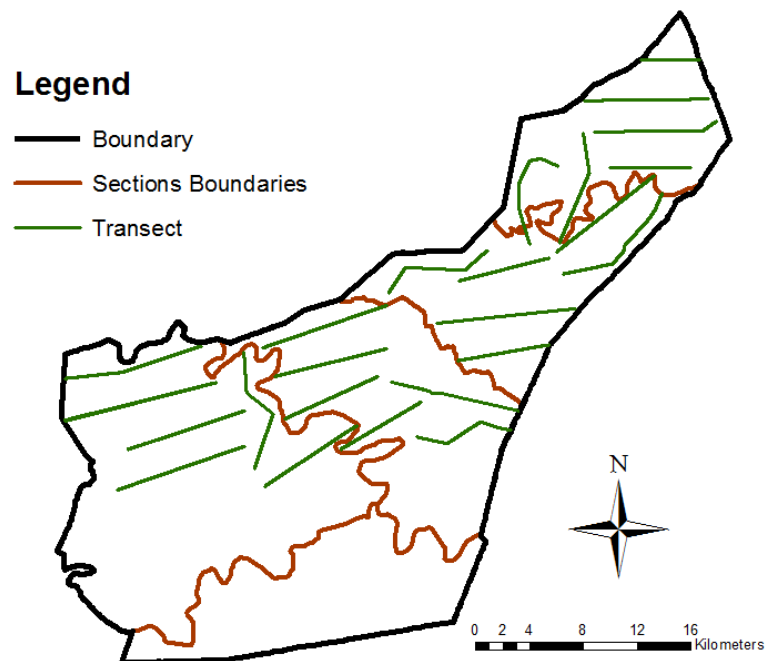
Figure 1. Locations of the transects and boundaries of the management sections in Hluhluwe-iMfolozi Park.

C. odorata was first found in Hluhluwe-iMfolozi Park in 1961. Its high dispersing potential of its seeds allowed it to disperse efficiently and in high number in the north of the park (te Beest 2010). The peak of the invasion was reached during the first half of the 2000s according to the fraction of the landscape invaded. In 2001, 20% of the area of the park was invaded. This period of high density of invasion was followed by a clearing period. The Alien Invasive Plant's Clearing program was started in 2004 by Ezemvelo KwaZulu-Natal (KZN) Wildlife (the provincial conservation authority) and the KZN province government. The clearing was mainly mechanical and chemical and continued from 2004-present (te Beest 2010).

Sampling
To estimate the distribution of *C. odorata* and of the different ungulates in the reserve, I walked 24 in average 2 meters large cut line transects, ranging from 4 to 11 kilometers in length, with an average of 8 km and a total length of all transects of 190 km (see Figure 1). This data was previously collected using the exact same method from August to October 2004. I did this sampling again from October to November 2014. This happened just after the bi-annual game census for which the transects are cut in order to be easily walked. Moreover, dung counts would have been more difficult during the wet season when dung decays much faster and dung beetles remove the excrements. Two or more observers walked transects with an experienced guard to reduce the error of identification of dung. Observers counted *C. odorata* and ungulate dung per 5 m plot all along transects. I followed the exact same protocol as in 2004, to allow for comparison (see Figure 2).
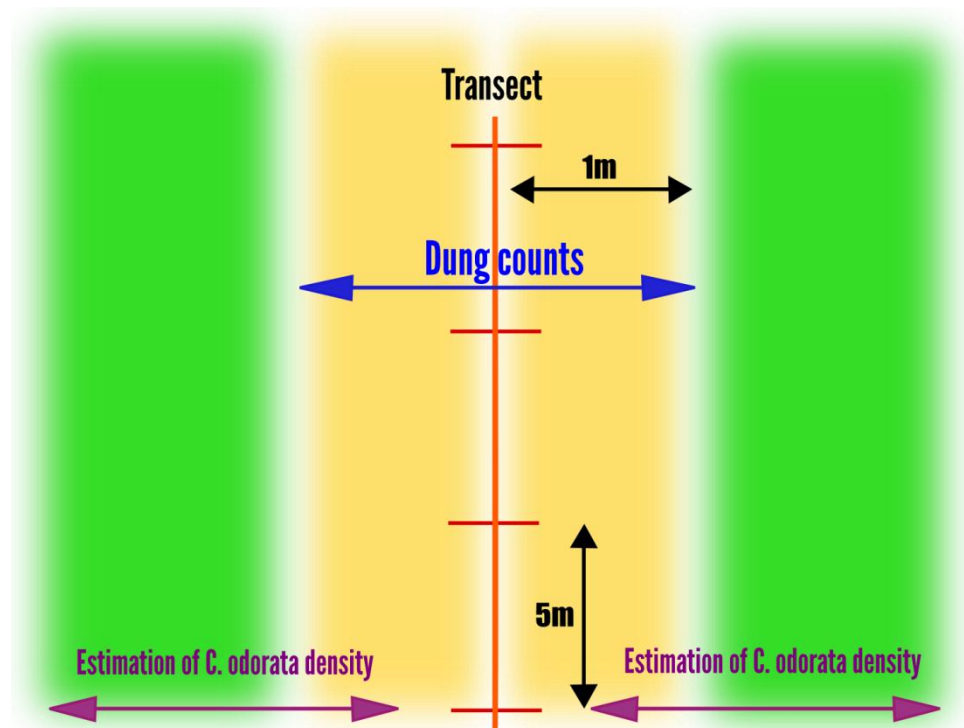
Figure 2. Sampling method on the transects. Dung abundance and *C. odorata* density is estimated for every 5 meters plot.

C. odorata was recorded according to 6 density classes (according to the Braun-Blanquet scale) on the left and the right of the transect line; the counts ranged from 0 (no plant) to 5 (a dense infestation creating an impenetrable wall of shrub; see Table 2). In 2004, this density was estimated every 50 meters. In 2014, I estimated the density every 5 meters (Figure 2). To make those values comparable, I averaged 2014 densities for every 50 meters and rounded this value to the superior density class value. For each plot, each year, I kept the maximum of the left and right values to proceed on statistical analyses.

Density class	Cover estimate	Observation
0	0%	No observation
1	1-5%	Few individuals present
2	6-25%	Low density
3	26-50%	Medium density
4	51-75%	High density, bushes still separable
5	>76%	Very high density, continuous monoculture

Table 2. Definition of the density classes of *C. odorata*.

I counted dungs per ungulate species within 1 m on each side of the transect (Figure 2). As white rhino uses territorial dung heaps (named middens) that are scattered, I counted all white rhino dung I could see from the transect (Cromsigt et al. 2009).

All along the transects I also estimated the presence of grazing lawns. A grazing lawn is a 10*5 meters quadrat where more than 75% of the vegetation cover consists of short (<5 cm) lawn species, growing stoliniferously (e.g. *Dactylotenium austral*, *Urochloa mossambicensis*). I also recorded in the same way areas that were burnt in the preceding

months (on one side of the transect or both). Those two environmental parameters are important to consider because they can influence my results. Lawns can be strongly selected by some grazers. Burning opens areas, change the vegetation composition and reduce the chance that the transect is used as a track by the ungulates.

For each plot, each transect, I have then the density of *C. odorata*, the abundance of dungs for the 14 studied species, the presence/absence of burn areas and grazing lawns.

Data analysis
Invasive plant distribution and habitat association analysis
Using the program ArcGIS and the package "sp" (Bivand et al. 2013) in R (R Development Core Team 2014), I mapped the distribution of *C. odorata* in 2004 and 2014. I also mapped the change in invasive density between 2004 and 2014 in a 0.005 decimal degrees cell-sized raster. For all plots I calculated the difference in density class between the two years. As many plots are in one cell of the raster, I calculated for each cell the median of the difference of density class.

I used a high resolution remotely sensed (LANDSAT) vegetation map of the park, which used woody cover to categorize habitats (Meyer 1999):
-   Woodland (dense woody cover)
-   Riverine (dense woody cover along rivers)
-   Grassland (almost no woody cover)
-   Open Savanna (grassland with scattered trees)
-   Others (reeds, water, soil and sand)
I here assumed that habitats are fairly stable in time and that this map is still valid in 2004 and 2014.
I divided the density of *C. odorata* in three categories: No Invasion (density 0), Low Invasion (densities 1 to 3) and High Invasion (4 and 5). I then looked at the association between habitat types and invasion density class using a Principal Component Analysis (PCA) and the "ade4" in R (Dray and Dufour 2007). I used the result of this analysis to interpret habitat selection analysis which won't take habitat type as a fixed effect. Knowing if the invasion is more constrained to one type of habitat could help to know if a habitat selection pattern is due to the invasion or to the selection the habitat where the invasive shrub is present.

Habitat selection analysis
I specified the habitat selection behaviors of each species using Resource Selection Functions (RSFs). RSFs are any functions proportional to the probability of use of a resource unit by an animal (Boyce et al. 1999, Manly et al. 2002). The used habitat is described by all variables that are thought to take part in habitat selection. A variable can either be a numeric continuous variable (distance to a resource), or a factor (absence/presence of the resource).
For each used resource units (scored 1) is attributed an equal number of randomly available units (scored 0). Each unit is described by n variables $x_1, x_2, ..., x_n$. Following Boyce et al. (1999), a RSF can be modeled by a log-linear model (Equation 1).

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_n x_n) \qquad \text{(Equation 1)}$$

Where β_k the habitat selection coefficient for the variable k.
Following Manly et al. (2002), I estimated those coefficients using a logistic regression (Equation 2).

$$\tau(x) = \frac{w(x)}{1+\text{w}(x)}$$ (Equation 2)

With $\tau(x)$ following a binomial distribution (used resource units being 1, available random units being 0).

For each used unit (a 5m plot with dung in it), for each species, I created a random location in any plot of any transect unit in the same management section of the park (1 of 4). I did this to constrain the habitat randomly available to an animal responsible for a certain dung sample to an area that was reasonably accessible to that animal within a season without long-distance migration.

For each species, for each year, the selection of habitat was explained and predicted by the 6 levels of density of *C. odorata* as fixed effects. I included two random effects (Gillies et al. 2006): burnt plots nested within each transect and lawn presence nested within each transect. This logistic regression was conducted using the *glmer* function from the "lme4" package in R (Bates et al. 2014). An *anova*, using the package "car" (Fox and Weisberg 2011), was used to check if the *C. odorata* density significantly affects the habitat selection behavior.

Recolonization-desertion analysis
Having abundance data of ungulates dungs per plots for a year of high density of invasion and a year of low invasion allowed me to check if *C. odorata* is the parameter affecting habitat selection in our study. Making the assumption that the habitat didn't change between 2004 and 2014, I could have a look if a decline in *C. odorata* density leads to an increase or a decline in dung abundance in the plots (called respectively recolonization or abandon later in the text).
For each plot I calculated the rate of change in dung abundance for each species between 2004 and 2014. According to the results of the habitat selection analysis for the different *C. odorata* density classes in 2004, I divided all the 5 meters plots over two or three *C. odorata* density zones for each ungulate species separately. These zones were based on the 2004 RSFs results. The zones grouped *C. odorata* density classes with similar RSF score; No invasion or low density (Zone 0), medium and/or high density (Zone 1) and if needed high density (Zone 2). To define the zones, I used an AIC based model selection using the *anova* function. The different models that I compared in the AIC model selection grouped density classes differently in the different zones. I selected the model with the lowest AIC and thus the zones included in this model (see Table 5).
Using the *lmer* function of the "lme4" package in R, I then explained how the change in dung abundance from 2004 to 2014 depended on the *C. odorata* density zone as a factorial fixed effect, using the burn data and the lawn data nested within transect number as random effects.
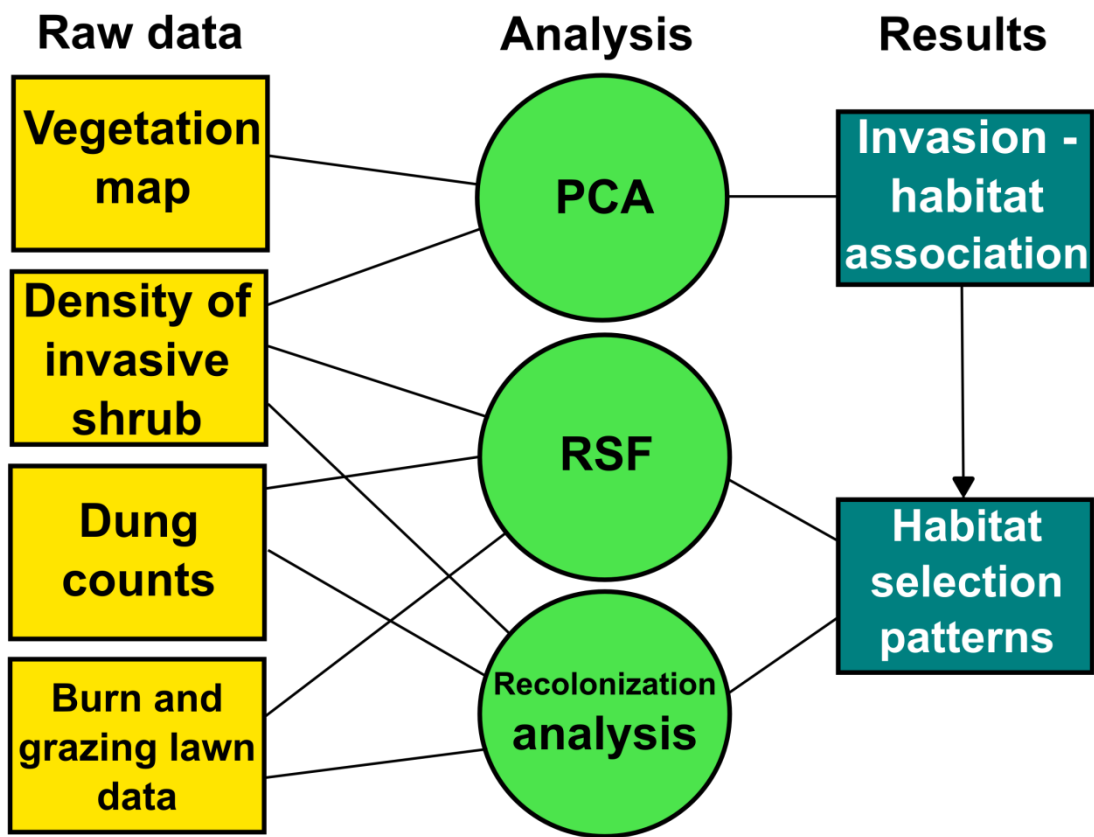
Figure 3. Flow chart of the analyses.

Results

C. odorata *distribution in 2014 versus 2004*

The invasion of *C. odorata* is concentrated in the North with pockets of invasion in the central part of the Park (Figure 4). The invasion is lower in 2014. In the North, the density of the invaded plots strongly declined between 2004 and 2014 (Figure 5). No plots of high density of *C. odorata* (density class 4 or 5) is found in 2014 on the transect, meaning that there were no longer impenetrable patches of *C. odorata* present in this year (Figure 6).
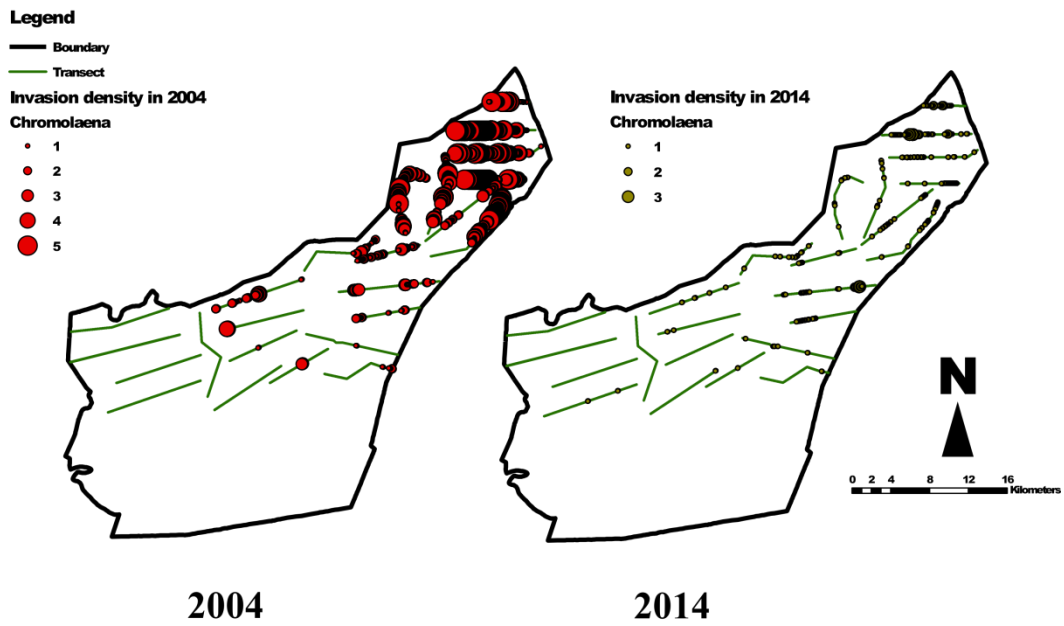
Figure 4. Invaded plots and their density in 2004 and 2014. Each dot is a 5*2 meters plot located on a transect.

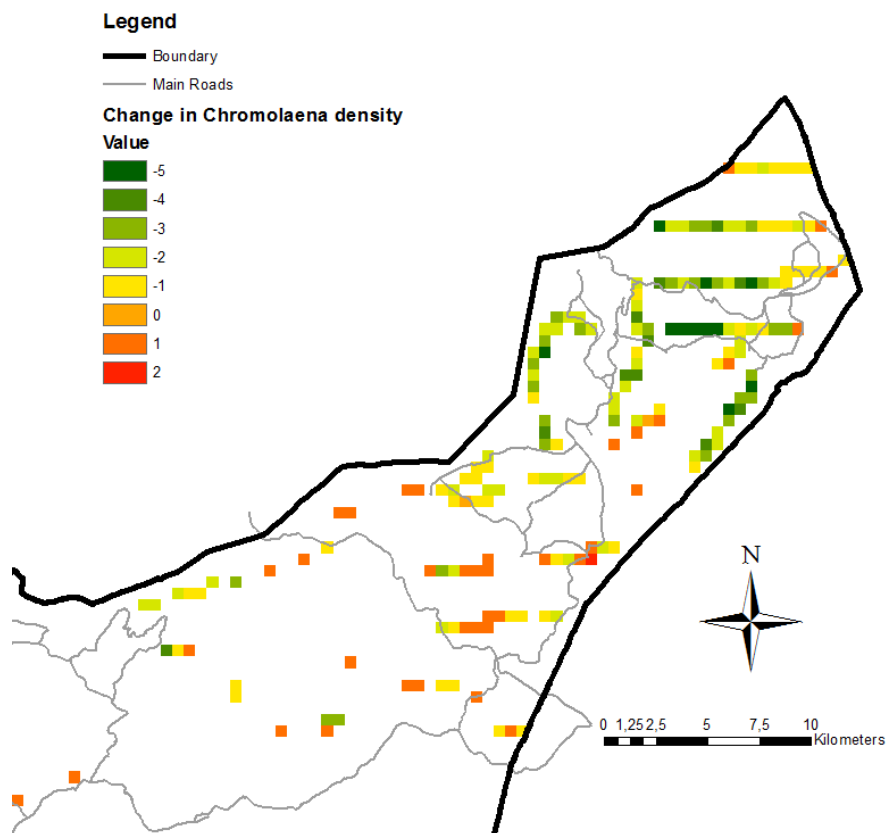

Figure 5. Change in Chromolaena odorata density between 2004 and 2014. Each pixel contains the median of the change in density of C. odorata between 2004 and 2014 for the plots included. Are not considered the plots that have never been invaded.
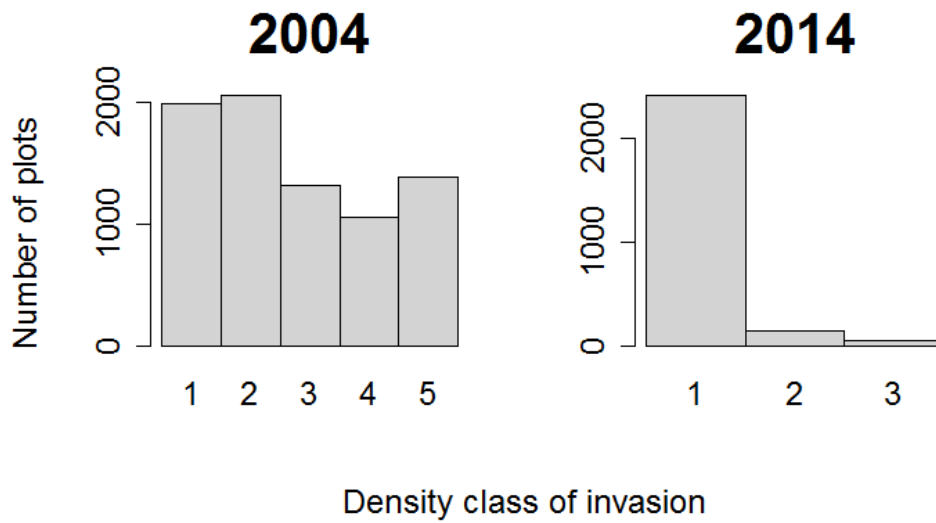
Figure 6. Comparaison of the number of plots of each *C. odorata* density class between 2004 and 2014.

Association between C. odorata *density classes and habitat type*
The first two axes of the PCA plotting habitat types and *C. odorata* density explain respectively 27 and 21 percent of the deviance. The low and high invasion density classes are associated with riverine habitat and woodlands. The non-invaded plots were more strongly associated with grasslands. Open savannas and other habitats were not clearly associated with any of the density classes (Figure 7).

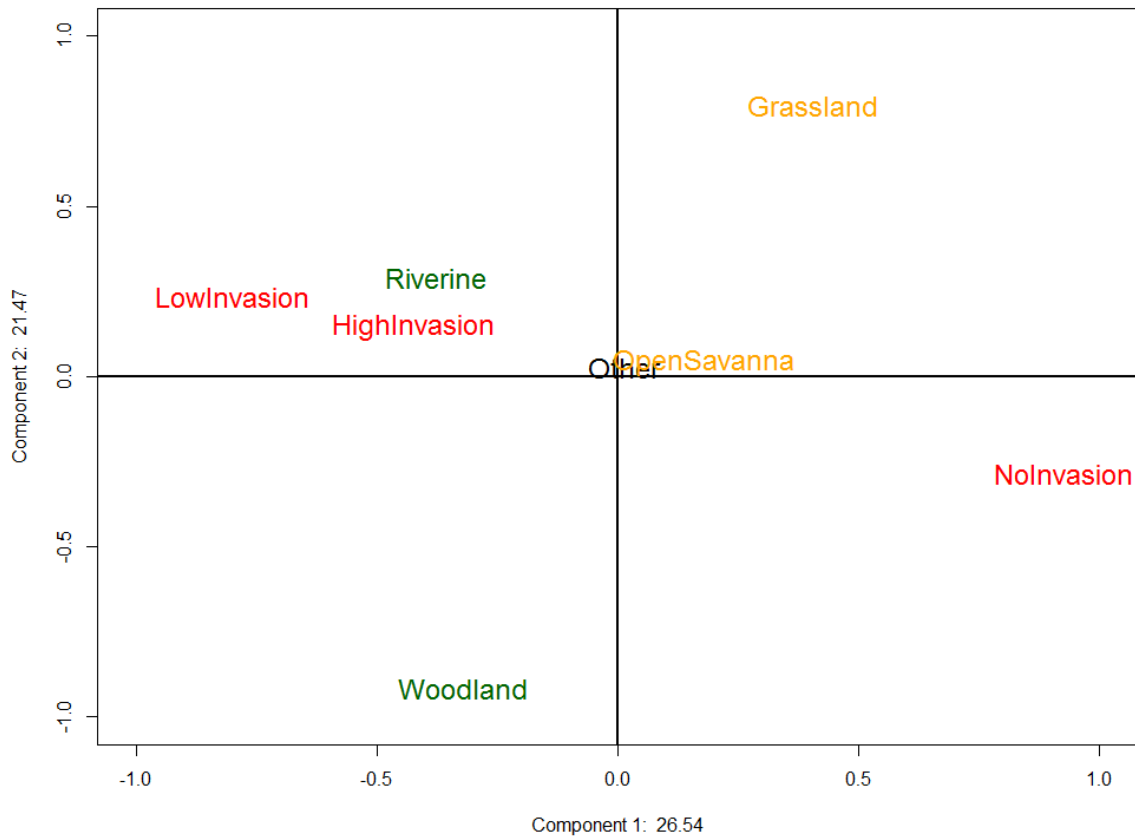**Combinations between habitat and invasion by Chromolaena odorata**

Figure 7. . PCA analysis showing habitat combinations between different density of invasion (red), closed habitats (green) and open habitats (orange).

Herbivore selection for C. odorata *density classes*

Species	Plot visited - 2004	Dung counted - 2004	Plot visited - 2014	Dung counted - 2014
Black Rhino	250	250	340	344
Buffalo	11362	13418	7776	8842
Bushpig	1868	2064	806	900
Duiker	84	100	316	352
Elephant	3952	4308	4290	4462
Giraffe	2248	2256	2802	2852
Impala	3520	8720	3490	6078
Kudu	280	288	262	272
Nyala	2260	2538	2310	2664
Warthog	3368	3828	700	758

Species	Plot visited - 2004	Dung counted - 2004	Plot visited - 2014	Dung counted - 2014
Waterbuck	0	0	20	20
Wildebeest	3340	5142	694	970
White Rhino	742	746	1094	1104
Zebra	4372	4724	770	812

Table 3. Description of the data. Number of plots visited by the species according to dung presence and number of dung counted for all plots. The distribution of those plots for each species are plotted in Appendix 2, 3 and 4.

The RSFs results are presented in Table 4 and detailed for the species and year for which the *anova* showed a significant impact of the presence of *C. odorata*. Buffalo, warthog, nyala and zebra avoided the high density patches of *C. odorata* in 2004 (see Figure 8). Impala and wildebeest show the same tendency, however the high avoidance at density 5 is not significant. In contrast, bushpig selects habitats of medium density of *C. odorata* in 2004. Elephant seem to do the same in 2014. The other were not significantly impacted by *C. odorata* (black and white rhinos, giraffe) or this impact is not clear (elephant in 2004). Some of the models also did not converge because of a lack of data (duiker, waterbuck and kudu).
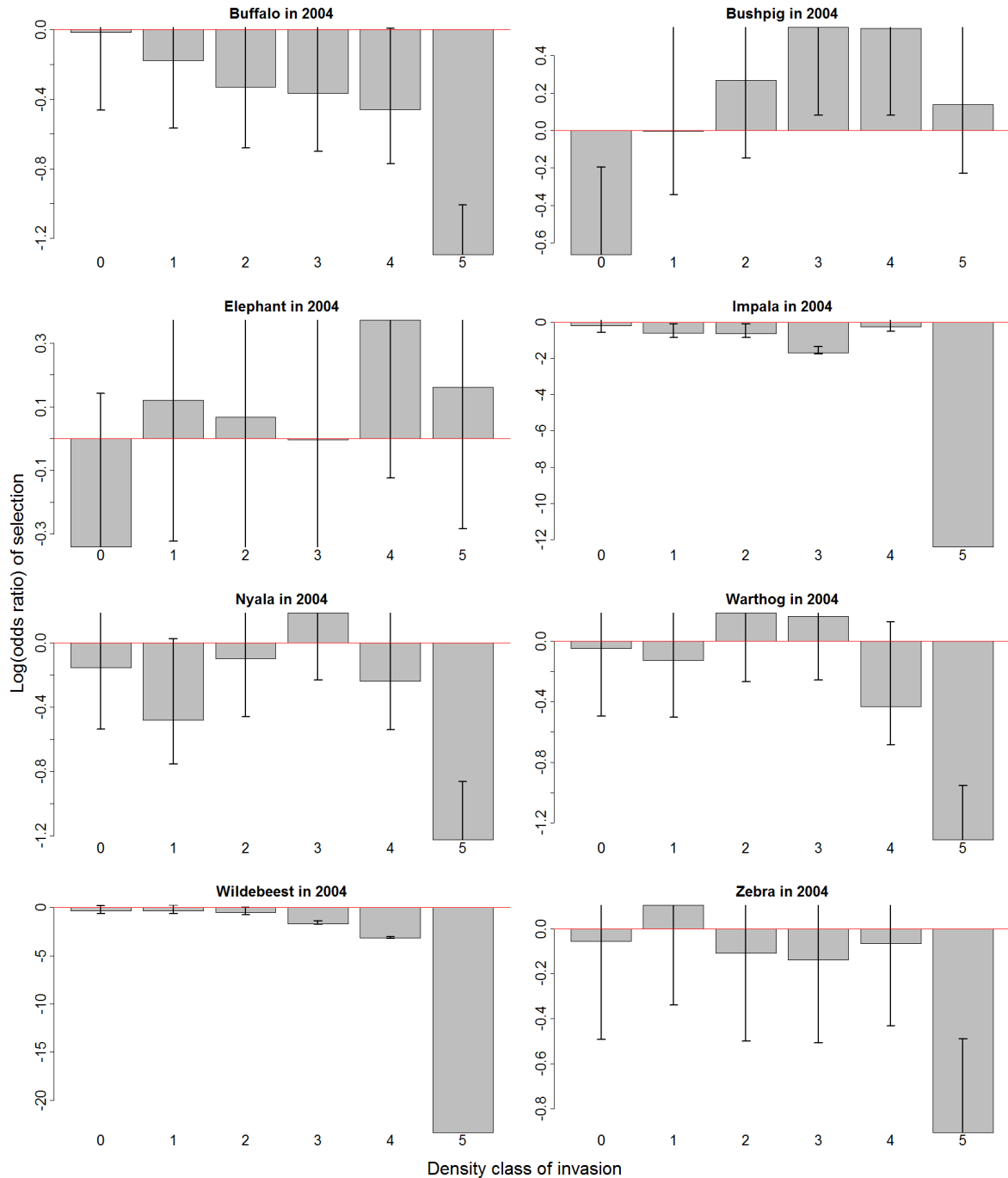
Figure 8. Pattern of habitat selection in 2004 observed in the RSFs analysis. Other tendencies have not been plotted as the model didn't show any significant pattern.

Change in herbivore presence from 2004 and 2014 in previously densely invaded plots
I studied the recolonization/abandon of the plots that were densely invaded in 2004 for the species cited above. The AIC values comparing models with various Zone 1 definitions are presented in Table 5 as well as the best models estimates. Buffalo and nyala recolonized 2004 highly invaded habitats ("Density 5"). Warthog, wilderbeest and zebra also recolonized those habitats ("Density 4 and 5"). Bushpig show the opposite and reduce their use of patches with medium *C. odorata* density in 2004. Elephant and impala don't show any pattern. The results are shown in Figure 9.
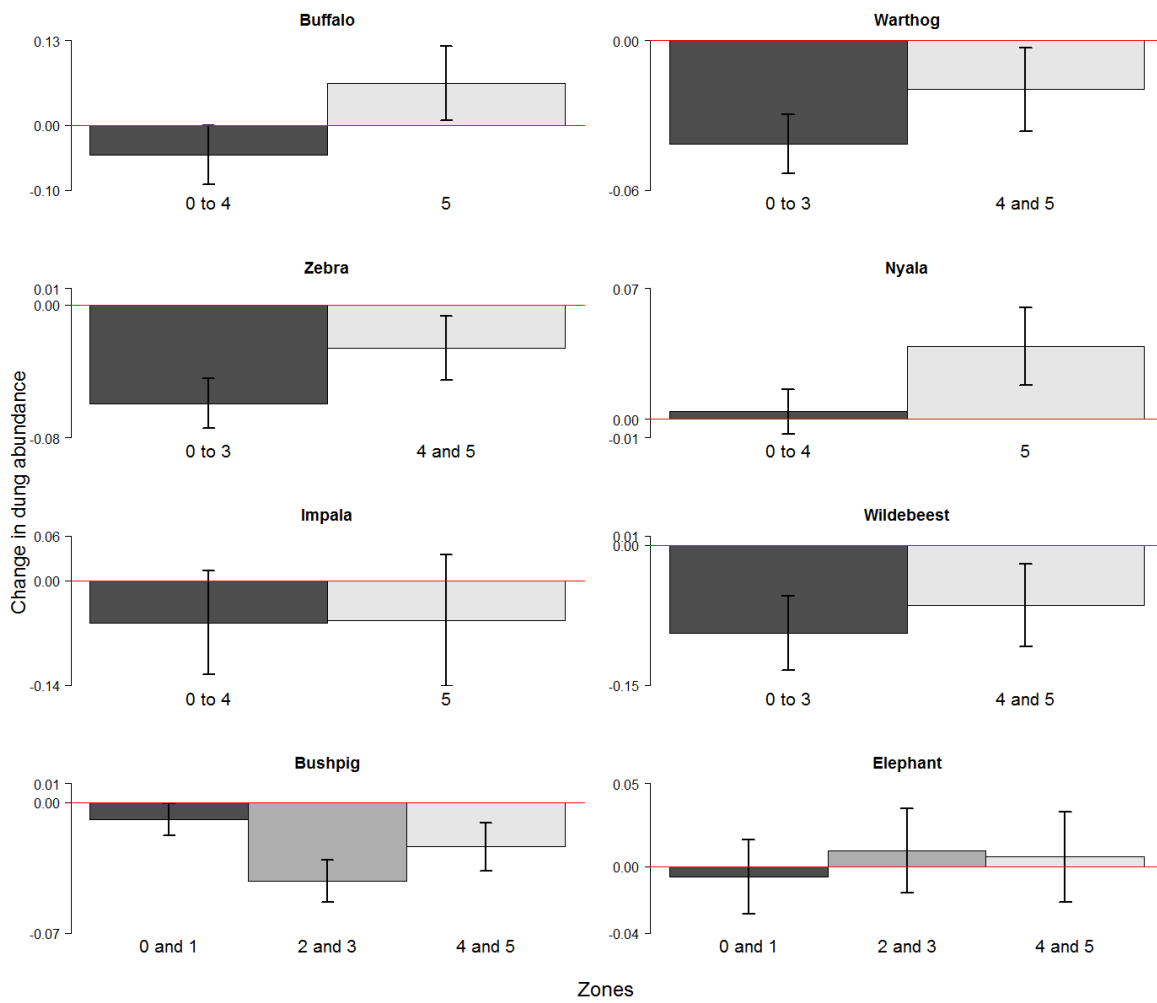
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Figure 9. Recolonization/desertion analysis. Change in abundance are plotted with confidence intervals (error bars) according to the zones defined following the RSFs analysis and model selection.

Species	Year	Anova	Density	Estimate	SE	Z value	P-value
Black Rhino	2004	0.3					
Buffalo	2004	< 0.001 ***	0	-0.02	0.10	-0.16	0.87
			1	-0.16	0.10	-1.65	0.10
			2	-0.31	0.11	-2.94	0.003 **
			3	-0.35	0.13	-2.72	0.006 **
			4	-0.44	0.14	-3.17	0.002 **
			5	-1.28	0.17	-7.58	< 0.001 ***
Buffalo	2014	< 0.001 ***	0	0.57	0.54	1.05	0.30
			1	0.57	0.11	5.45	< 0.001 ***
			2	0.65	0.44	1.47	0.14
			3	0.93	0.53	1.76	0.08
Bushpig	2004	< 0.001 ***	0	-0.66	0.27	-2.46	0.013 *
			1	0.66	0.22	2.94	0.0032 **
			2	0.93	0.19	4.91	< 0.001 ***
			3	1.21	0.24	5.06	< 0.001 ***
			4	1.21	0.25	4.86	< 0.001 ***
			5	0.80	0.24	3.35	< 0.001 ***
Bushpig	2014	0.016 *	0	-0.28	0.35	-0.81	0.42
			1	0.83	0.27	3.12	0.0018 **
			2	-0.18	0.69	-0.27	0.79
			3	22.42	$78e^3$	0	0.99
Duiker	2014	X					
Elephant	2004	< 0.001 ***	0	-0.34	0.14	-2.40	0.016 *
			1	0.46	0.12	3.93	< 0.001 ***
			2	0.41	0.12	3.35	< 0.001 ***
			3	0.34	0.14	2.37	0.018 *
			4	0.71	0.15	4.89	< 0.001 ***
			5	0.50	0.14	3.53	< 0.001 ***
Elephant	2014	< 0.001 ***	0	0.15	0.43	0.36	0.72
			1	0.64	0.12	5.38	< 0.001 ***
			2	0.98	0.36	2.72	0.007 **
			3	0.93	0.73	1.28	0.20
Giraffe	2004	0.56					
Giraffe	2014	0.99					
Impala	2004	0.009 **	0	-0.19	0.19	-0.98	0.33
			1	-0.40	0.26	-1.57	0.12
			2	-0.42	0.31	-1.39	0.16
			3	-1.48	0.43	-3.47	< 0.001 ***
			4	-0.04	0.39	-0.11	0.91
			5	-12.22	125	-0.10	0.92
Impala	2014	< 0.001 ***	0	-0.23	0.58	-0.39	0.69
			1	1.70	0.27	6.26	< 0.001 ***
			2	2.10	1.43	1.47	0.14
			3	-13.1	2760	-0.005	0.99
Kudu	2004	0.99					
Kudu	2014	X					
Nyala	2004	0.0016 **	0	-0.16	0.17	-0.92	0.36

Species	Year	Anova	Density	Estimate	SE	Z value	P-value
			1	-0.33	0.21	-1.54	0.12
			2	0.06	0.20	0.29	0.77
			3	0.34	0.23	1.51	0.13
			4	-0.08	0.26	-0.31	0.75
			5	-1.07	0.31	-3.50	< 0.001 ***
Warthog	2004	0.0053 **	0	-0.05	0.08	-0.58	0.56
			1	-0.08	0.19	-0.41	0.68
			2	0.23	0.18	1.30	0.19
			3	0.21	0.24	0.89	0.38
			4	-0.38	0.33	-1.15	0.25
			5	-1.26	0.37	-3.43	< 0.001 ***
Warthog	2014	0.31					
Wildebeest	2004	< 0.001 ***	0	-0.33	0.23	-1.42	0.16
			1	0.01	0.24	0.05	0.96
			2	-0.177	0.28	-0.64	0.52
			3	-1.34	0.38	-3.47	< 0.001 ***
			4	-2.84	0.77	-3.69	< 0.001 ***
			5	-23.00	129	-0.18	0.86
Wildebeest	2014	0.04 *	0	-0.35	0.54	-0.65	0.52
			1	1.84	0.90	2.05	0.04 *
White Rhino	2004	0.94					
White Rhino	2014	0.26					
Zebra	2004	0.04 *	0	-0.06	0.10	-0.553	0.58
			1	0.16	0.15	1.075	0.28
			2	-0.05	0.15	-0.360	0.71
			3	-0.08	0.19	-0.440	0.66
			4	-0.01	0.23	-0.045	0.96
			5	-0.85	0.27	-3.082	0.002 **
Zebra	2014	0.90					

Table 4. Results of the RSF models predicting the ungulates habitat selection as a function of the density of *C. odorata*. The estimates are relative to the intercept, which is density class 0. SE: Standard Error. Significance: $0.05 \geq$ "*" $> 0.01 \geq$ "**" $> 0.001 \geq$ "***". Only the models for which the effect of the invasion is significant (using the anova function) are detailed. The 2004 significant models are plotted in Figure 6. The 2014 significant models are plotted in the appendix.

Species	Zone 1	AIC	Zone	Estimate	SE	T value	P-value
Buffalo	5	66114	0	-0.047	0.023	-2.04	0.06
			1	0.111	0.018	6.21	< 0.001 ***
Buffalo	4 – 5	66120					
Buffalo	3 to 5	66133					
Bushpig	3	-9818					
Bushpig	2 – 3	-9840	0	0.009	0.004	-2.20	0.039 *
			1	-0.033	0.004	-7.72	< 0.001 ***
			2	-0.014	0.005	-2.81	0.005 **
Bushpig	2 to 4	-9832					
Bushpig	1 to 5	-9824					
Elephant	3	25823					
Elephant	2 – 3	25819[1]	0	-0.006	0.011	-0.57	0.577
			1	0.016	0.007	2.30	0.022 *
			2	0.012	0.008	1.45	0.148
Elephant	2 to 4	25817					
Elephant	1 to 5	25823					
Impala	5	100119	0	-0.056	0.035	-1.63	0.11
			1	0.0033	0.028	0.12	0.91
Impala	4 – 5	100119					
Impala	3 to 5	100119					
Nyala	5	13336	0	0.004	0.006	0.66	0.515
			1	0.035	0.009	3.93	< 0.001 ***
Nyala	4 – 5	13343					
Nyala	3 to 5	13351					
Warthog	5	7459					
Warthog	4 – 5	7454	0	-0.042	0.006	-7.03	< 0.001 ***
			1	0.022	0.006	3.45	< 0.001 ***
Warthog	3 to 5	7460					
Wildebeest	5	44446					
Wildebeest	4 – 5	44441	0	-0.094	0.020	-4.76	< 0.001 ***
			1	0.030	0.010	2.86	0.004 **
Wildebeest	3 to 5	44442					
Zebra	5	11437					
Zebra	4 – 5	11430	0	-0.059	0.007	-7.99	< 0.001 ***
			1	0.033	0.007	4.97	< 0.001 ***
Zebra	3 to 5	11438					

Table 5. Results of the recolonization analysis predicting the change in dung abundance between 2014 and 2004 as a function of a group of densities of *C. odorata* (Zones defined using the RSFs analysis). The estimate are relative to the intercept, which is Zone 0. SE: Standard Error. *Significance: 0.05 ≥ "*" > 0.01 ≥ "**" > 0.001 ≥ "***".* Are detailed the models selected using AIC. [1]: This model has been chosen because of a problem of calculation of the significance of the fixed effects in the lowest AIC model. The AIC model selection has been made using the function *anova*, those two models were not significantly different.

Discussion

With the comparison of the location of the invaded plots and their invasion densities, my results suggest that even though its distribution didn't change, its density was reduced between 2004 and 2014 by the intense clearing program. I also show that the *C. odorata* invasion was mostly associated with woodlands and riverine habitats, which confirms Macdonald and Frame (1988) and te Beest et al. (2015) observations.

The habitat selection analysis revealed two different patterns: the avoidance of high density class patches (density 4 and 5 mainly) or the selection of medium density class patches (density 3 and 4). I used those results to define Zone 1 in two ways in the recolonization/abandon analysis. In the first case, Zone 1 was comprised of high density patches; in the second case, Zone 1 was comprised of medium-invaded patches, and I created a Zone 2 for the high density patches in this case. I show that species that avoided high density patches (nyala, buffalo, warthog, wildebeest and zebra) tend to either recolonize those patches more than others or to leave them less after clearing. The species (bushpig) that selected for medium-invaded patches are abandoning those plots more than the others. Some other species (impala and elephant) ignore the invasion.

My results show different patterns that can be explained, according to the usual habitat selection patterns of the studied ungulates and that *C. odorata* is mostly restricted to woodlands and riverine habitats. Of the species living in woody habitats and browsing (giraffe, kudu, nyala), only the nyala shows a significant avoidance of the invasive shrub with both RSFs and the recolonization analysis. This effect seems to be restricted to patches of density cover between 75 and 100% (density 5). With the knowledge that Smith (2010) found woody vegetation to be lower in height in presence of *C. odorata*, and in the absence of other studies showing different results, I would make the assumption that the food availability for browsers is not modified by *C. odorata*. Those elements allow me to conclude that it is the physical barrier of a dense concentration of shrub that impacts the habitat selection of the nyala.

C. odorata invades open grass dominated spaces less than what would be expected if this process was random. Therefore, the avoidance of invaded patches by species selecting open spaces cannot be explained without the results of the recolonization/abandon analysis. In this perspective, all grazers are effectively avoiding high density patches of *C. odorata*. An explanation for this could be the physical barrier again, but also the change in grass diversity caused by the invasion (Smith 2010). This result is not so homogeneous for the four concerned species: buffalo, warthog, zebra and wildebeest. Buffalo is recolonizing previously high density patches and leaving the other patches. However, warthog, wildebeest and zebra are less numerous in 2014, showing an abandonment pattern for all habitats, even though they still show that they use Zone 1 more than Zone 0 in 2014, relative to 2004. I explain these results in two ways. First, buffalos are mostly selecting grasslands, according to the literature; however, observations in the park and other studies (e.g. Ryan et al. 2006) suppose also a selection for more closed habitats, possibly to protect the herd from predators. This assumption could furthermore explain the selection for low invaded habitats in 2014 as a habitat bias. Buffalos are mainly affected by *C. odorata* as a physical barrier. The other grazers are less numerous, they might have suffered from an increased predation in the park (the number of lions and wild dogs increased significantly between 2004 and 2014). But the clearing of *C. odorata* opened habitats where their predators could have hidden when densely invaded. I suppose than predation pressure

might also be affected by the invasion.

Mixed feeders, such as impalas (mostly grazers in the park; Cromsigt et al. 2009) or elephants (mostly browsers at the end of the dry season, before migration from North to South) show hardly interpretable patterns in RSF in terms of ecology, or show the total absence of pattern in the recolonization/desertion analysis. Impalas are mostly present in the South and Central part of the park where the invasion is much lower, accounting for a spatial separation of this species and the invaded areas in the park (see Appendix 3). In contrast, elephants were mostly in the invaded areas when the data were collected, where their capacity to browse foliage in higher trees and to walk through the thickest patches allow them to ignore the invasion.

However, *C. odorata* affected bushpig in a different way. In contrast to the other species, bushpig selected for medium-invaded patches and declined in the plots in 2014 that were previously invaded. I hypothesize that this species avoids predators by hiding and using the *C. odorata* thicket as a shelter. Bushpig is also the species for which the dung records have diminished the most between 2004 and 2014. The clearing of *C. odorata* might have also increased the predation pressure on this species even more than in the case of zebras, warthogs and wildebeests. Such a "thicket effect" on predation risk could be checked using camera traps in further studies.

The case of rhinos and giraffes could be potentially explained. The ability of giraffes to feed on the leaves of high branches might allow them to ignore the invasion at a lower level. Avoiding the high density patches is not necessary for them, the possibility to browse on the trees in those areas being still possible. No significant effect is either found for rhinos (both black and white). The use of middens by those species to defecate reduces the data availability, implies that dung location is not linked to habitat utilization and makes the habitat selection analysis using dungs difficult.

Dumalisile (2008) studied the impact of the same invasive, in the same park, on large mammals, on an experimental basis. The two studies have in common an avoidance of the invaded patches by buffalos; however, Dumalisile (2008) also observed a constant visitation of nyalas and warthogs between non invaded, invaded and clear patches. The plots of this experiment were chosen in one single habitat and according to duration of invasion and not density, and tracks were recorded. The difference of scale (my study using the scale of the entire park) and methods between the two theses makes the comparison of results difficult.

My study points out that having a population of an invasive species out of control in an environment can do more than locally change the vegetation structure. *C. odorata* is neither eaten by nor deadly toxic to animals; it is then only its physical presence that affects herbivores in their habitat selection. Savannas are highly heterogeneous systems, functioning on the basis of numerous interactions and dynamic equilibriums (e.g. Skarpe 1992). Such modifications in habitat selection could lead to other environmental changes. However, as most species are affected by high density patches of invasion, a good choice to make in terms of management would be to focus clearing programs on those patches. Trying to get rid of lower density patches might get too expensive and complicated knowing that they are not impacting most of the ungulates.

Acknowledgments

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Appendix
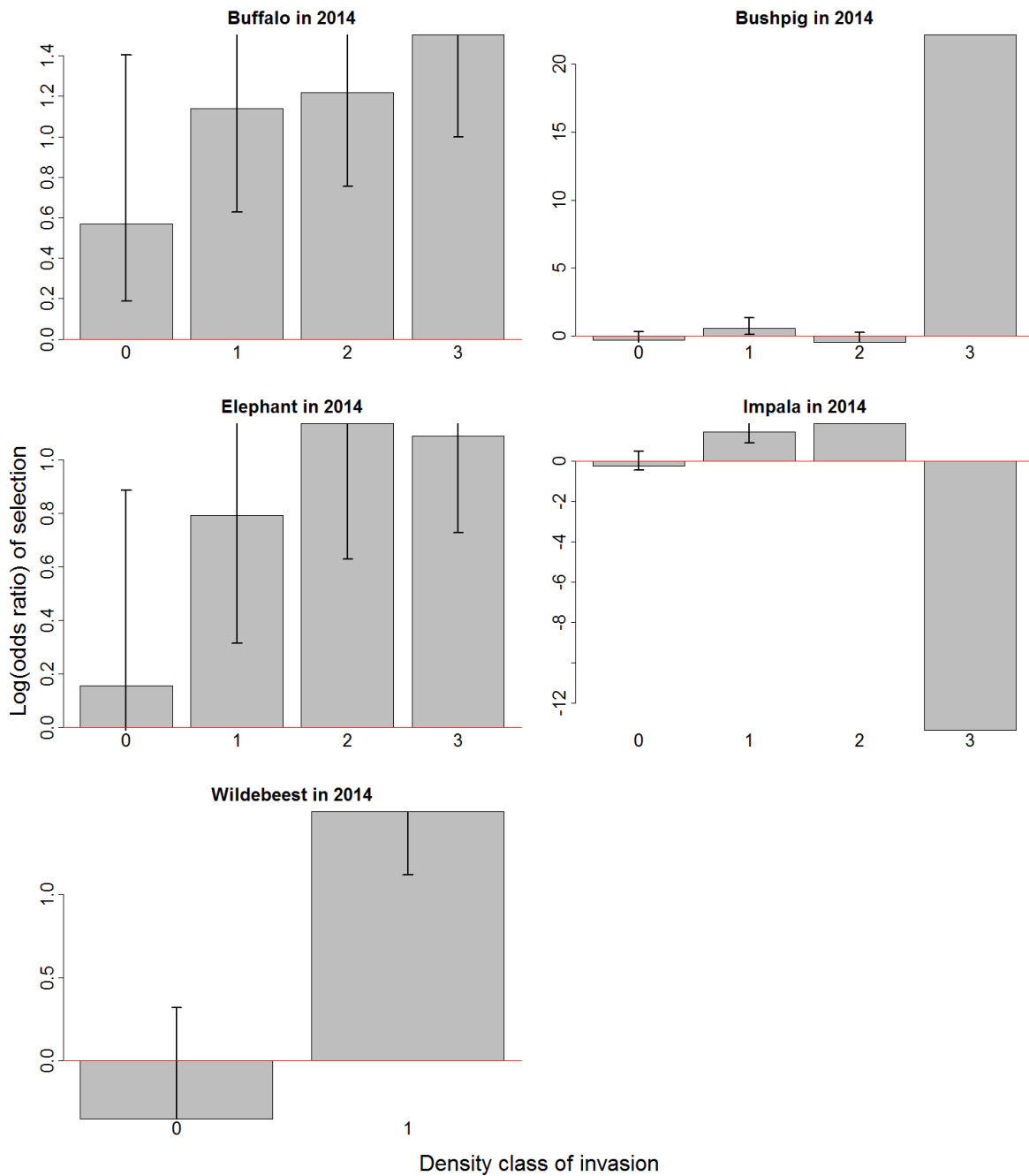
Appendix 1. Pattern of habitat selection in 2014 observed in the RSFs analysis. Other tendencies have not been plotted as the model didn't show any significant pattern.
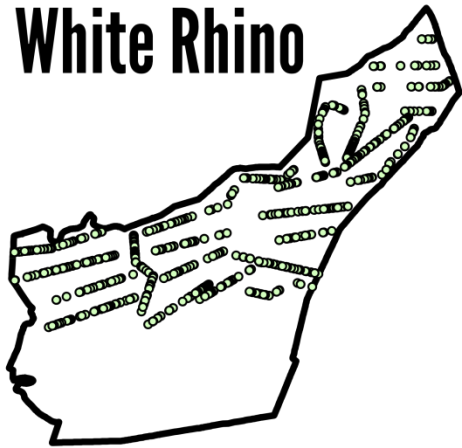
Buffalo
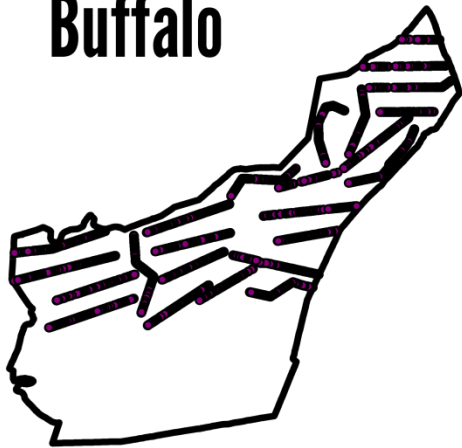
Warthog

Waterbuck

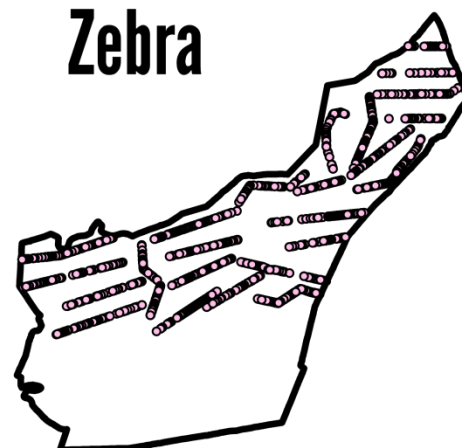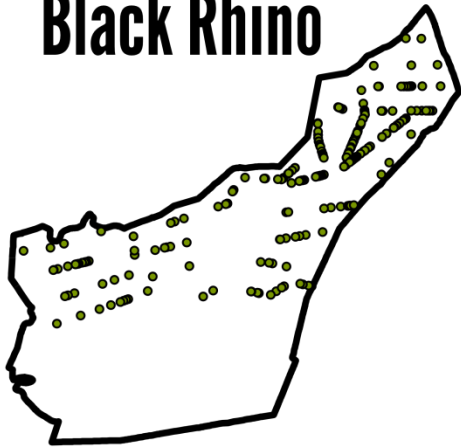# White Rhino

Wildebeest

Zebra

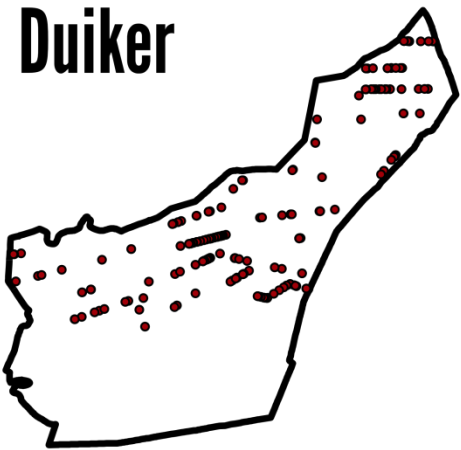Appendix 2. Plots where were present the different grazers of the park in 2004 and 2014.

Black Rhino

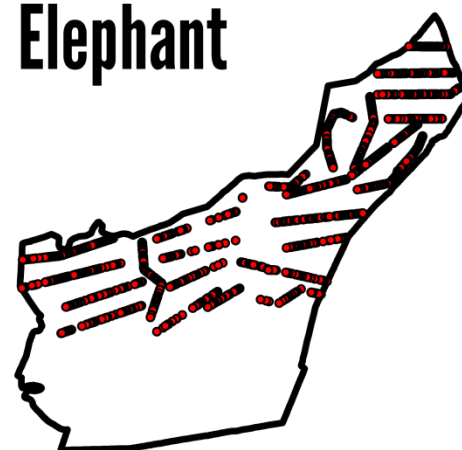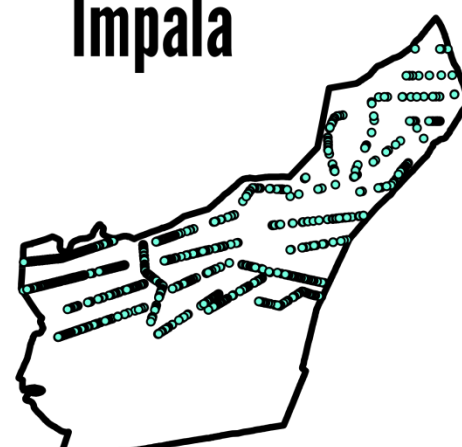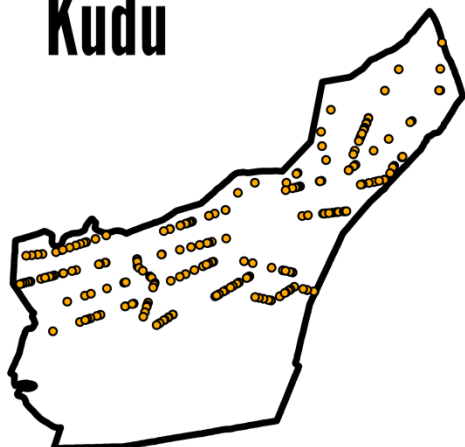**Bushpig**

Duiker

Elephant
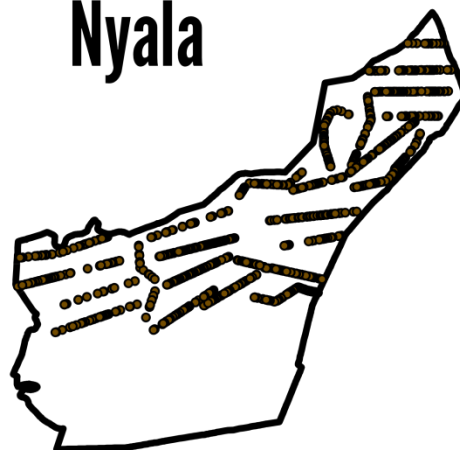
Giraffe
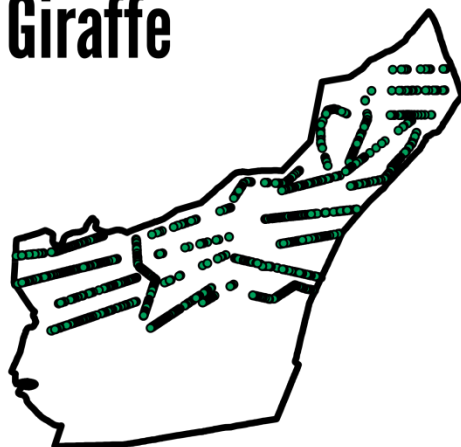
Impala

Appendix 3. Plots where were present the different browsers of the park in 2004 and 2014 (part 1).

Kudu **Nyala**

Appendix 4. Plots where were present the different browsers of the park in 2004 and 2014 (part 2).

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