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**Effects of *Chromolaena odorata* on mammalian biodiversity in Hluhluwe-iMfolozi
Park, South Africa**

by

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**Submitted in partial fulfilment of the requirements for the degree
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Supervisor: Dr. Michael J. Somers

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I declare that the dissertation, which I hereby submit for the degree Magister Scientiae (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature

A handwritten signature in black ink, appearing to read 'Dumalisile', written over a horizontal line.

Date

11 February 2008

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ABSTRACT

This study investigated the effects of the Triffid weed *Chromolaena odorata* on small and large mammals in Hluhluwe-iMfolozi Park. *C. odorata* is a widespread invasive alien plant that poses threat to the highly maintained natural vegetation in HiP and most other protected areas in KwaZulu-Natal. Following the opinion that the effects of invasive alien plants on all levels of biodiversity need to be recognised for their effective control, we compared small and large mammal species richness and diversity between areas with differing *C. odorata* invasion durations, areas with differing clearing times and an area with no history of invasion as a control area. Small mammal trapping was done using Sherman live traps and mark-recapture techniques. Track counts were used to estimate large mammal species abundance, richness and diversity. The control area had higher small mammal species richness and diversity than the invaded areas, which suggests that invaded areas were not suitable habitats for small mammals. It was also found that small and large mammal species richness and diversity decreased with the increase in invasion duration,

which shows that the more time *C. odorata* is left to establish the more disturbance it causes to the habitat. We found the uninvaded treatment to have the highest diversity of large mammal species than all the invaded treatments, which suggests that large mammalian species show some degree of avoidance to the invaded areas. We also found that there were significant differences between the treatments with regard to large mammal species diversity indices. Some of the large mammalian species appeared to neither avoid nor prefer invaded areas. It is hypothesized that they use invaded areas to hide away from predators as most of them fall prey to many carnivores. Also, *C. odorata* invaded areas could provide suitable shelter from climatic extremes. The treatments cleared of *C. odorata* showed an increase in both small and large mammalian species richness and diversity, suggesting that clearing of this plant helps in rehabilitation of the ecosystem. However, large mammal species composition in the cleared treatments remained different to pre-invasion state, which suggests that the habitat may remain changed for a long time after clearing. Managers of conservation areas should therefore prioritise alien plant removal in order to maintain healthy ecosystems.

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CHAPTER 1

Effects of *Chromolaena odorata* on mammalian biodiversity in Hluhluwe-iMfolozi Park, South Africa

Introduction

Conservation of biodiversity has gained a great deal of attention and has become an objective of most conservation, governmental and nongovernmental organizations and many individuals (Redford & Richter 1999). Conservation biologists recognize biodiversity as an issue that involves more than just species diversity or endangered species, but also genes, populations, communities, ecosystems, and landscapes whereby each organizational level exhibits complex composition and function (Noss 1990; Redford & Richter 1999). According to Redford & Richter (1999) biodiversity refers to the variations amongst living organisms, the ecological complexes in which they naturally occur and their interactions with each other and with their surrounding environment. Therefore, biodiversity conservation should focus on the need to conserve the multitude of ecological patterns and processes that maintain the full tribute of living organisms and the natural systems that support them (Angemeier & Karr 1994). However, losses of biodiversity due to a variety of factors have been recognized. It is therefore imperative that threats that face the different aspects of biodiversity conservation be recognised. The ever-increasing human densities account for most of the biodiversity losses (Folke, Holling & Perrings 1996; Redford & Richter 1999; McKee *et al.* 2003). This study focuses on the threats that face mammalian biodiversity, with special focus on invasive alien plants.

A multitude of factors that affect both small and large mammalian populations have been identified. Fire has long been known to severely modify small mammal habitat in that it results in a reduction in food supply and cover (Bowland & Perrin 1988). Small mammals are very sensitive to changes in their habitats (Avenant 2000) and any kind of disturbance to these habitats would therefore be reflected on small mammal populations. Vegetation cover, food availability and shelter from predators are important factors that render a habitat suitable for small mammals (Fuller & Perrin 2001). Disturbance of small mammal habitats therefore results in the habitats being uninhabitable to small mammals. These disturbances may result from use of fire (Christian 1977; Salvatori *et al.* 2001) and

high grazing intensities by herbivores (Grant *et al.* 1982; Salvatori *et al.* 2001), which result in changes in vegetation cover affecting small mammal populations. Webala *et al.* (2006) found that the combined effect of livestock grazing and fire incidences could have been major limiting factors on small mammal species diversity as they reduced the understorey vegetation in Mukogodo forest, Kenya. Other factors that have an impact on small mammal habitats and thus small mammal populations include disturbances resulting from farming activities such as crop cutting (LoBue & Darnell 1959) and natural disturbances such as floods and hurricanes (Klinger 2006).

Large mammalian species select their habitats according to their ability to provide the four factors required for their survival; which are food, water, shelter from climatic extremes and protection from predators (Sinclair 1977). Disturbed habitats lack one or all of these factors and this affects large mammalian populations. Most disturbances to large mammalian habitats result from anthropogenic activities. Wilson & Johns (1982) for example, found that forest logging had a substantial effect on plant species composition, which in turn resulted in changes in mammal species composition. Heydon & Bulloh (1997) found that selective logging adversely affected two mousedeer species in northern Borneo, as these frugivorous species had to switch to browsing due to diet constraints resulting from logging. Other factors such as intense hunting pressure (Lopes & Ferrari 2000; Laurance *et al.* 2006) and roads that run through areas inhabited by mammalian species (Laurance *et al.* 2006) also affect large mammalian populations. Forest clearing for agricultural purposes has resulted in changes in forest composition, which has impacted large mammalian species inhabiting these forests, as the secondary vegetation that comes after the clearing might not provide sufficient food items (Wilkie & Finn 1990). One of the key threats that face biological diversity is alien species invasion (Chornesky & Randall 2003). Rated as the second largest threat after habitat destruction (Sharma, Raghubanshi & Singh 2005a), invasion by alien species has become a major concern for biodiversity conservation.

Alien species, as defined by Raghubanshi *et al.* (2005), are non-native, exotic plant and animal species occurring outside their natural adapted ranges. They may become invasive when introduced deliberately or unintentionally into new areas, where they tend to establish, invade and out compete native species (Raghubanshi *et al.* 2005). Invasion by

these exotic species is amongst the most important global scale problems experienced by natural ecosystems (Sharma, Singh & Raghubanshi 2005b), thus they have become the subject of much interest, largely because of the damage done by some (Williamson 1999.)

According to Raghubanshi *et al.* (2005), invasive species may result in loss of biodiversity including species extinctions, changes in hydrology and ecosystem functioning. In fact, biological invasions have been known as the cause for more species extinctions than have resulted from climatic changes caused by humans (D'Antonio & Vitousek 1992). Invasive species may reduce or displace native plant species, thereby altering the physical characteristics of a habitat (Gratton & Demo 2005), and animal species (Schofield 1989). Also, invasive species have negative affects on food webs in many ways, including the alteration of the quantity and/or quality of food, changing food accessibility or vulnerability to predators (Zedler & Kercher 2004). Sax & Brown (2000) and Sharma *et al.* (2005b) suggest that invasive species perform better in their introduced ranges than in their native ranges because they lose most of their enemies during recolonization, and they encounter assemblages of species that have not specialized to interact with them (Sax & Brown 2000). The impacts of invasive species on native biodiversity range from the genetic to the ecosystem level (Higgins *et al.* 1999; Vilà *et al.* 2003).

Invasions by alien plants have had some major consequences in most ecosystems, which include alterations in soil nutrient balance, competition among plants for water and changes in habitat suitability for native communities, particularly in pristine ecosystems (Higgins *et al.* 1999; Vilà *et al.* 2003). Case studies from around the world have shown that alien plant invasions can also lead to an increase in flammability (Anable, McClaran & Ruyle 1992), thus threatening native plant species (Musil 1993; Meyer & Florence 1996), and changes in habitat suitability for native animal species (Allan *et al.* 1997). Vitousek & Walker (1989) found that invasion by the nitrogen-fixing *Myrica faya* onto young lava flows in Hawaii alters the nature of the ecosystem development following volcanic eruptions. D'Antonio & Vitousek (1992) found that the effects of alien grasses on the local scale ecosystem functioning are significant, and are becoming increasingly important on regional and global scales. Sharma *et al.* (2005b) have recognized an increasing realization of the ecological costs resulting from biological invasions. In South Africa, *Chromolaena*

odorata is categorised as one of the most problematic alien plants that must be controlled (MacDonald *et al.* 2003).

Chromolaena odorata (Linn.) R.M. King and H. Robinson, commonly known as Siam weed (Muniappan & Bamba 2000; Ikuenobe & Anoliefo 2003) or Sandanezwe (MacDonald 1983), is a perennial semi-lignified pioneer plant with an extensive root system and leaves with essential oils. It occurs naturally in habitats below 1000 m of altitude, where it is most suitable, from southern Florida to Northwest Argentina as well as Caribbean Islands. It is typically a pioneer plant of secondary succession, which may reach a height of 10m in forests (Zachariades & Goodall 2002).

However, *C. odorata* is amongst the most important invaders in the world and has been ranked as the second most problematic plant that requires prioritisation in South Africa (Robertson *et al.* 2003). *C. odorata* is capable of rapidly invading clearings and persisting until shaded by overgrowth of taller vegetation. It is a prolific seed bearer, common in most habitats except undisturbed rain forest and arid regions, where it is either uncommon or completely absent and disperses very rapidly by wind, water, and animal transport (Tallamy 2004). It does not invade pasture nor compete successfully with plantation crops, and is never the target of specific weed control measures. The reduced aggression is due to attack by a large complex of insects, other arthropods and diseases, together with competition with other plants. In its native habitat, it is therefore controlled by these biotic factors.

Although it may die or lose its leaves during the dry season, *C. odorata* populations recover rapidly when the summer rains come (Zachariades & Goodall 2002). This plant is highly flammable and burns even when green in midsummer (MacDonald 1983). It is considered a serious weed in many areas such as undisturbed forests and natural reserves (Muniappan & Bamba 2000). *C. odorata* negatively affects biodiversity by suppressing indigenous grassland and savanna vegetation through physical smothering and allelopathy (Zachariades & Goodall 2002).

Chromolaena odorata invasions have negatively impacted the ecotourism and trophy hunting potential of conservation in South Africa by reducing game populations and visibility (Zachariades & Goodall 2002). Conservation areas are also under pressure from surrounding communities, as they tend to extend grazing lands to reserves because they

have lost their land to *C. odorata* (Zachariades & Goodall 2002). Throughout the subtropical areas of KwaZulu-Natal, *C. odorata* has had a massive deleterious effect on indigenous vegetation and has invaded nearly all the protected areas in KwaZulu-Natal (MacDonald 1983). *C. odorata* has also reduced the availability of the over-exploited and threatened indigenous plant species that are used in traditional medicine (Zachariades & Goodall 2002).

In the Hluhluwe Game Reserve *C. odorata* was first identified in 1961 and was well established by 1970 (MacDonald 1983). This plant has been seen as the most serious threat to the long-term maintenance of natural vegetation in HiP, and is the most widespread alien invader in the park (MacDonald 1983). Despite clearing by the Department of Water Affairs and Forestry (DWAF) since 1998, the area invaded in HiP continued to increase. In 1998 mapping exercises indicated that there were approximately 2 100 ha of dense *C. odorata* infestations. Between 1998 and 2001 control work (initial and follow up) was done over a similar area, but by 2001, a further mapping exercise indicated that there were 5 600 ha of dense infestations. Most of these infestations occurred through areas with light to medium infestations becoming heavily invaded, although in some cases it was due to lack of follow-up work, resulting in cleared areas becoming re-invaded. A *Chromolaena* clearing project was initiated in 2004 in HiP under Working for Water. This project is responsible for clearing the plant and provides follow-up work as required.

Although they are known to have severe negative consequences for biodiversity (Higgins *et al.* 1999; Sakai *et al.* 2001), the effects of invasive alien plant species on native species, such as small and large mammals, are not well documented. The functioning of the ecosystem is an important aspect of biodiversity conservation and the direct monitoring of small mammals has been shown to be a relatively quick and cheap method of indicating the health of the ecosystem (Avenant 2000). Changes in small mammal habitats are associated with changes in their diversity, and the ecological disturbance of these habitats is associated with decrease in small mammal species richness (Avenant 2000). Avenant (2000) found that the domination of an indicator species, low species richness and low diversity in small mammal populations, were useful tools which indicated disturbance on the primary producer level.

However, along with habitat changes by fire and grazing, the effects of invasive plant species on small mammal communities are unknown (Decher & Bahian 1999). A few studies have attempted to measure the impact of invasives on small mammal populations. Ayensu (1974) found a negative impact by an invading neem tree *Azadirachta indica* on the native plant and rodent populations and other faunal organisms inhabiting the Accra Plains of Ghana. According to Ayensu (1974), the progressive occupation by the neem trees may diminish or destroy the equilibrium between the native flora and fauna in the Accra Plains. Ayensu (1974) concludes that the phenomenal adaptation of the neem tree to the Accra Plains may eventually result in partial or total elimination of the native flora and fauna. Decher & Bahian (1999) detected no effect specifically relating to the presence of *A. indica* on small mammals, in the same Accra Plains. They suggested that this was due to their inability to sample areas with pure stands of *A. indica* due to the clearing taking place and also their small sample size. However, they concluded that dense stands of the invading *A. indica* may adversely affect small mammals, as they rarely caught small mammals in traps placed next to dense stands of neem trees (Decher & Bahian 1999).

The effects of invasive alien species on large mammalian species are also not well documented, although large mammalian herbivores are perceived as characteristic parts of the world's ecosystems (Holland & Detling 1990). Although no research has been done yet, the decline in the numbers of black rhinoceros *Diceros bicornis* in HiP is associated with the invasion of their habitats by *C. odorata*. It is predicted that the carrying capacity of black rhinoceros in HiP has decreased by as much as 200 since the invasion of *C. odorata*, and now the population has declined from 325 individuals in 2000 (Reid *et al.* 2007) to 246 individuals in 2006 (HiP Internal report). Studies on the invasion of key black rhino habitats by invasive plants such as *C. odorata* are underway (Reid *et al.* 2007). *C. odorata* has also impacted on other species such as the Nile crocodile *Crocodylus niloticus* (Leslie & Spotila 2001). The Nile crocodile is among the high-profile species whose habitat is threatened by *C. odorata* invasions in the Greater St. Lucia Wetland Park (GSLWP), found in the Maputaland Centre of Endemism northern KwaZulu-Natal (Leslie & Spotila 2001). *C. odorata* was found to have a shading effect on the Nile crocodile's nesting sites, which reduced incubation temperatures resulting in shaded sites being below the pivotal temperature for Nile crocodiles thus producing a female-biased sex ratio that

may eventually result in extirpation of the Nile crocodile in GSLWP (Leslie & Spotila 2001).

An understanding of aspects of invasions by alien species that change ecosystem-level properties could be useful in conservation biology (Vitousek *et al.* 1997). Also, the documentation of the impact of these species on native communities is vital for their management and to determine whether removal of these invasives results in the restoration of the native communities (Gratton & Denno 2005). Weinstein *et al.* (1997) suggest that the removal of alien invasive plants to restore natural habitats is becoming an important tool in the management of natural resources and ecosystem functioning. This study therefore investigates the broader effects of a serious invasive plant (*Chromolaena odorata*) on small and large mammal communities and also determines whether the removal of this invasive plant helps in the restoration of the ecosystem. The aims and objectives for this study are therefore to:

- Determine the effects of *C. odorata* invasions on small mammal diversity in HiP
- Determine the effects of *C. odorata* invasions on large mammal diversity in HiP
- Determine whether clearing of *C. odorata* helps in restoring native mammal communities in HiP
- Provide management recommendations for the management of alien plants in HiP

Study area

Hluhluwe-iMfolozi Park is situated in the northern escarpment of the KwaZulu Natal province, South Africa. The park covers an area of approximately 960 km², comprising of the 300 km² Hluhluwe section in the north and the 660 km² iMfolozi section to the south lies between 28°00' to 28°26' S and 31°43' to 32°09' E. Four large rivers flow through the park: the Hluhluwe river in the north with its three major tributaries the Manzibomvu, Mansiya and Nzimane rivers; the Nyalazi river to the south; and the black and white Umfolozi rivers further south (Whateley & Porter 1983). The climate in HiP is coastally modified and varies according to the topography. Annual rainfall is seasonal and mostly falls between October and March, with a mean of 985 mm in the high altitude regions in

the north and a mean of 650 mm in the low-lying western areas. Annual temperatures range from 13°C to 35°C, occasionally dropping below freezing point in the low lying valleys during clear winter nights, and are strongly influenced by altitude.

HiP has a diverse topography and range of soil types and therefore supports a number of different habitat types. The park falls in the savanna biome of South Africa and lies within the Lowveld subcategory of the Tropical bush savanna types and Zululand Thornveld, which is a subcategory of the Coastal Tropical Forest (Acocks 1988). The park also contains 60% of the total area of savanna found within protected areas in KwaZulu-Natal, and houses over 1 200 plant species. The northern Hluhluwe part of the park is covered with remnants of coastal scarp forest dominated by wild plum *Harpephyllum caffrum* and white stinkwood *Celtis africana*. Riverine valleys contain a fringing forest that includes species of fig *Ficus spp.*, weeping boer-bean *Schotia brachypetala* and stands of tamboti *Spirostachys africana*. The rest of the reserve is a complex mixture of open grasslands, savannas and thick bush. Savanna woody species include the shrub *Dichrostachys cinerea* and various species of *Euclea* and *Acacia*. Grasslands range from tall fire prone communities dominated by *Themeda triandra* to short highly grazed lawn grass communities featuring such species as *Urochloa mossambicensis*, *Digitaria longiflora* and *Dactyloctenium australe*. Prominent trees in savanna areas include the marula *Sclerocarya birrea* and *Acacia burkei*. There is some turnover in species between the two ends of the park with *A. karroo* and *A. nilotica* being common in Hluhluwe but replaced by *A. tortilis* and *A. nigrescens* in iMfolozi. Whateley & Porter (1983) give a detailed classification of vegetation types.

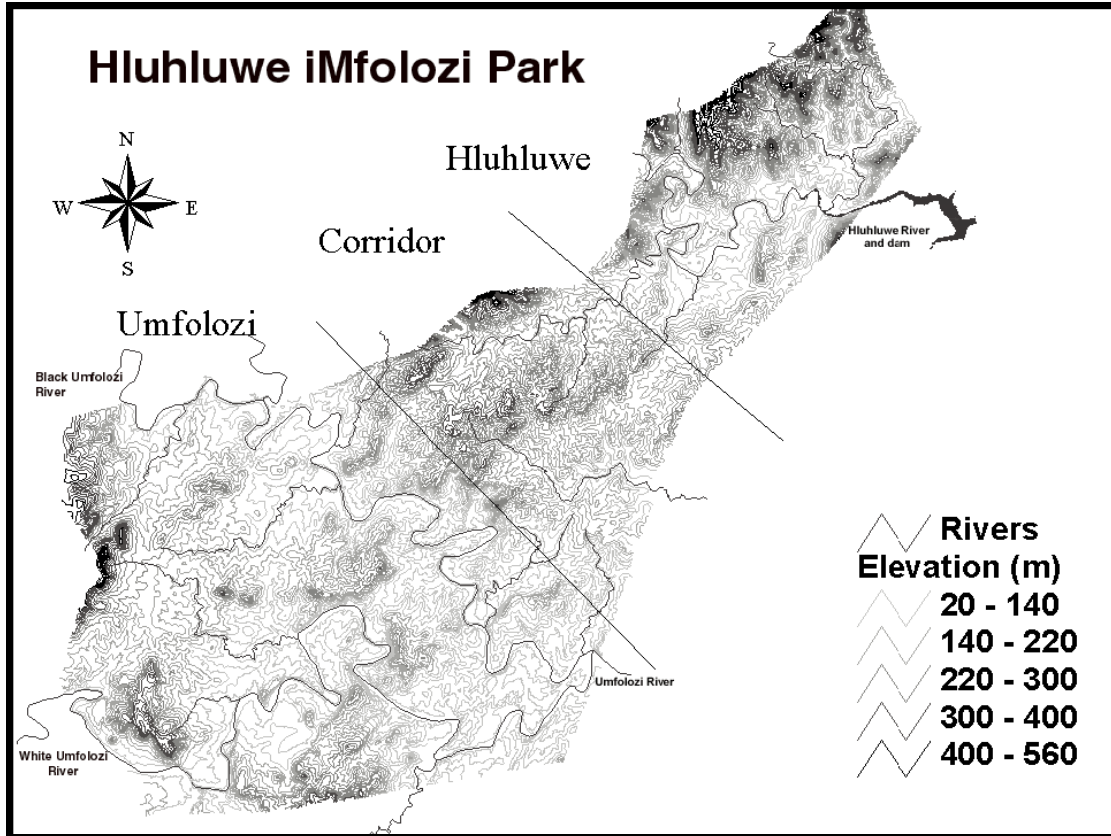


Fig.1. Map of Hluhluwe-iMfolozi Park showing the three areas in which it was once divided into, contours and major watercourses as adapted from Waldram (2005).

There has been a large amount of change in the amount of the various vegetation types in the reserve over the last 70 years and bush encroachment has been extensive despite efforts to control it. It appears that bunch grass communities have also increased over the same period, out-competing short grass communities (Bond, Smythe & Balfour 2001). Causes of the bush encroachment are unclear (Skowno *et al.* 1999). However, the observed changes do indicate the presence of a dynamic ecosystem within the park. These changes have been compounded by the invasion by the trifid weed *Chromolaena odorata*.

HiP supports a large number of grazers, which include wildebeest *Connochaetes taurinus*, zebra *Equus quagga*, impala *Aepyceros melampus*, white rhinoceros *Ceratotherium simum*, warthog *Phacochoerus africanus* and buffalo *Syncerus caffer*. The major species of browsers are giraffe *Giraffa camelopardalis*, black rhinoceros *Diceros*

bicornis, elephant *Loxodonta africana*, kudu *Tragelaphus strepsiceros* and nyala *Tragelaphus angasii*. A full compliment of large carnivores (lion *Panthera leo*, spotted hyaena *Crocuta crocuta*, cheetah *Acinonyx jubatas*, leopard *Panthera pardus* and wild dog *Lycaon pictus*) occurs in the park and also a wide spectrum of other herbivores, carnivores, small mammals and other taxa.

The area that today includes the park is believed to have been originally occupied by nomadic khoi-san people, who possessed a skilled use of fire for the purposes of hunting, attracting game and modifying their environment (Lewis 1989; Price & Bowman 1994; Bowman, Walsh & Prior 2004). Evidence of their presence still remains in the form of cave paintings. Around the third century, Nguni tribes began to arrive in the area from the north. They had a more settled existence characterised by the tending of cattle and the farming of maize. Extensive archaeological sites in the park remain well preserved and include kraals and iron smelting sites, indicating that the area was continuously worked and inhabited. Among these Nguni tribes was a small clan of people that called themselves amaZulu, who settled in a valley some 40 km west of the present Umfolozi section and south of the white Umfolozi River. In the early 19th century the area was ruled by King Shaka who gained as much control of the tribes and formed the Zulu kingdom. The area between the two Umfolozi rivers were proclaimed as royal hunting grounds, which was likely to be the first form of wildlife protection in the area. It was during this period that European settlers and traders first came through and provided some of the early records of game in the area.

In 1895 the Hluhluwe and Umfolozi were proclaimed as game reserves, making them the oldest of proclaimed reserves in Africa. In 1898 the newly proclaimed reserves were victim to a rinderpest epidemic, which spread through Zululand and killed about 80% of cattle in this area. The rinderpest epidemic, combined with malaria and nagana resulted in a decrease in wildlife populations in many of the lower lying areas, including Umfolozi. The area between the two reserves, known as the corridor, was proclaimed as state land in 1950 from which time the two reserves were managed together as one unit. The corridor region was officially incorporated into the reserve in 1982 and fencing of the reserves commenced in 1964.

In 1919 there was an outbreak of nagana, which is a blood borne disease related to human sleeping sickness that effects cattle, horses and other domestic animals and is caused by the blood parasite *Trypanosoma*. It was thought that wild game acted as a reservoir of the blood parasite, which was then passed to cattle by tsetse flies *Glossina spp.* Nagana campaigns took place in and around the reserve from time to time between 1919 and 1954. A decision was made to cull all game within the reserve in order to eradicate the disease and 96 000 head of game were shot. Nagana was eventually brought under control through the use of flytraps and the extensive aerial spraying of the insecticide DDT, which was applied to the reserve between 1948 and 1951. More culling was carried out during the period 1959 to 1970 due to concerns expressed about overgrazing of the veld and to simulate the effect of absent predators. These culls focused on short grass grazers, such as warthog, which were thought to compete with white rhinoceros for food. From 1979 to 1984 a head of 20 000 grazers and browsers were removed during a drought in order to protect the veld and prevent starvation (Walker *et al.* 1987).

Historically Zululand was home to substantial herds of elephants, but by 1916 the population had gone down to zero due to Ivory trade. However, elephants were reintroduced to HiP from Kruger national park in 1979, with the aim to re-establish natural processes in the park that were formerly driven by elephants. It was thought that the absence of elephants for such a long time could have been the cause of the occurrence of bush encroachment, but despite numbers increasing to more than 300 in recent years any impact on bush encroachment has yet to be seen.

This study aims at investigating the effects that the invasive alien plant *Chromolaena odorata* can have on the species diversity and abundance of small and large mammals in Hluhluwe-iMfolozi Park; and to investigate whether the removal of *C. odorata* contributes in ecosystem restoration.

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CHAPTER 2

The changing effects of an alien invasive plant over time: small mammals as affected by *Chromolaena odorata*

Abstract

Invasive alien plant encroachment is known to result in severe losses of biodiversity which is why it is essential to recognize the impacts such plants have on native communities in order to ensure their effective and successful management. The effects of invasives on small mammal communities are not well documented. Nevertheless, small mammals are very sensitive to changes in their habitats, thus any changes in their habitats are reflected in their species composition. This study investigated changes in small mammal communities in areas with differing invasion durations of the invasive trifid weed (*Chromolaena odorata*) in Hluhluwe-iMfolozi Park, South Africa. Small mammal assemblages were compared between 1) areas with differing *C. odorata* invasion durations (*ca* 2 yrs, *ca* 10 yrs, *ca* 20 yrs), 2) areas that had been cleared of *C. odorata* at different times (*cl* < 2 yrs, *cl* 3-5 yrs) and 3) as a control, an area that had never been invaded. Increasing *C. odorata* invasion duration was found to decrease small mammal species richness and diversity indicating an unhealthy ecosystem. The cleared areas showed an increase in small mammal species richness and diversity when compared to invaded areas demonstrating that clearing the plant aids in the restoration of the habitat. However, as the area that had been cleared for 3-5 years displayed lower species richness and diversity than the area that had been cleared for less than two years, and because *C. odorata* populations recover very rapidly, it is essential that follow-up work is done on the cleared areas.

Introduction

Invasive alien species have become a major concern for the conservation and management of natural ecosystems (Soulé 1990). Invasion by exotic species is amongst the most important problems experienced by natural ecosystems globally and has resulted in change in habitat (Vilà *et al.* 2003), severe losses of native biodiversity and immense ecological costs (Sharma, Singh, & Raghubanshi 2005). Alien plant species occur at the expense of native flora and any drastic modifications of the flora are expected to be reflected in the

fauna (MacDonald 1983). It is therefore vital that the impacts of invasive species on native communities are recognized in order to, firstly, achieve effective management of these species and, secondly, to determine whether removal of these invasive species can result in the restoration of native communities (Gratton & Denno 2005).

Triffid weed (*Chromolaena odorata*) is amongst the most important plant invaders in the world and has been ranked as the second most problematic plant that requires prioritisation in South Africa (Robertson *et al.* 2003). It occurs naturally in most suitable habitats below 1000 m altitude from southern Florida to Northwest Argentina and is typically a pioneer plant of secondary succession (Leslie & Spotila 2001) that forms scrambling thickets and grows to a height of up to 6 m (McFadyen & Skarratt 1996). *C. odorata* forms dense stands and is capable of growing through the canopy of native trees and shrubs and overshadowing these (MacDonald & Frame 1988). The plant is highly flammable and burns even when green in midsummer (MacDonald 1983). It is a prolific seed bearer, and disperses very rapidly by wind, water, and animal (Tallamy 2004). It is the most problematic alien invasive plant in conservation areas of KwaZulu-Natal and poses a great threat to the highly maintained natural vegetation in Hluhluwe-iMfolozi Park (MacDonald 1983).

Small mammals are very sensitive to changes in their habitats, and ecological disturbances of the habitats are associated with decreases in small mammal species richness (Avenant 2000). Small mammal populations in woodland savanna are known to respond to environmental changes such as habitat quality, food, and cover (Monadjem & Perrin 1998). Also, the lack of floral diversity and vegetational homogeneity in small mammal habitats are known to affect small mammal species richness, diversity and abundance (Delany 1974; Fuller & Perrin 2001). Because *C. odorata* out-competes native vegetation, homogeneity of vegetation occurs and this is assumed to have effects on small mammal communities.

Few studies (e.g. Ayensu 1974; Decher & Bahian 1999) have attempted to measure the impact of alien invasive plants on small mammal communities, but without conclusive results. More recently, Mahlaba & Perrin (2003) concluded that alien weed infestations were amongst the factors that resulted in the low small mammal biomass recorded in Mlawula Nature Reserve, Swaziland. In western Montana, Ortega, Pearson, & McKelvey

(2004) found that invasions by the widely established exotic spotted knapweed *Centaurea maculosa* resulted in reduced potential native food resources for mice, leading to decreased indices of breeding productivity for mice in knapweed invaded areas. Small mammals are known to be useful indicators of environmental conditions (Mahlaba & Perrin 2003) and the monitoring of small mammal communities has been used as a quick and cheap method of indicating whether an ecosystem is “healthy” or not. Additionally, the monitoring results may facilitate the management of nature reserves and future development of natural areas (Avenant 2000).

Although much research has been undertaken on the effects of alien invasive plants on different forms of biodiversity, there is little known about how biodiversity recovers after the removal of alien invasive plants (Samways, Taylor & Tarboton 2005). This study therefore uses small mammal community characteristics as an indicator of disturbance occurring from *C. odorata* invasion, and also as an indicator to determine whether clearing of this plant aids in the restoration of the native ecosystem. This study aimed at determining the following:

- The effects of *C. odorata* invasions on small mammal diversity
- Whether the duration of invasion by *C. odorata* had more deleterious effects on small mammal diversity
- Whether *C. odorata* clearing is helping in restoring the ecosystem

Methods

Study area

Hluhluwe-iMfolozi Park (HiP), lies between 28°00' S and 28°26' S; 31°43' E and 32°09' E in the foothills of the South African escarpment and to the west of the coastal plain in central KwaZulu-Natal, South Africa. The park covers an area of approximately 960 km² comprising the 300 km² Hluhluwe section in the north and the 660 km² iMfolozi section in the south. The numerous hills and valleys found in this park have altitudes ranging from 60 m to 750 m (Whateley & Porter 1983). Consequently, the mean annual rainfall ranges from 985 mm in the high altitude regions of the north to 650 mm in the low-lying western areas. It falls mainly between October and March (Whateley & Porter 1983). The park lies within the Lowveld subcategory of the Tropical Bush Savanna types and

Zululand Thornveld, which is a subcategory of the Coastal Tropical Forest (Acocks 1988). Savanna woodland is the predominant vegetation type in the park. However, the savanna vegetation type does range from open fire maintained grasslands through open woodlands to densely encroaching woodlands, thicket, and closed woodlands. Evergreen forest and grassland are the remaining vegetation types of the park (Whateley & Porter 1983). The long-term monitoring of the vegetation in Hluhluwe has shown some structural changes in vegetation cover since it was proclaimed a protected area in 1895. The changes include increases in tree and shrub cover and invasions by alien plant species such as *C. odorata* (MacDonald 1983). HiP has a high faunal diversity (MacDonald 1983), which includes all the African megaherbivores and a wide spectrum of other herbivores, carnivores, small mammals and other taxa.

Study site selection

The work was done in the northern part of the Hluhluwe section of HiP, an area that appears to be optimal for *C. odorata* (MacDonald 1983). Historical maps of the status of *C. odorata* in the Park were analyzed. From these maps the duration of *C. odorata* invasion was determined and six treatments were selected. The six treatments were: 1) an area that had been invaded and not cleared for *ca* two years when the study commenced, 2) an area that had been invaded and not cleared for *ca* 10 years when the study commenced, 3) an area that had been invaded and not cleared for *ca* 20 years, 4) an area that had been invaded for more than 10 years and cleared between one and two years before the commencement of the study, 5) an area that had been invaded for more than 10 years and cleared between three and five years before the commencement of the study, and finally, as a control area, an area that had never been invaded. Areas cleared of *C. odorata* were cleared by means of hand pulling, cutting mature stems and applying an herbicide to stumps, and by applying a foliar spray to seedlings.

Small mammal sampling

Within each of the six treatments six trapping sites, spaced a minimum of 100m apart were selected, giving a total of 36 trapping sites. In each trapping site six Sherman live traps (3 cm x 3.5 cm x 9 cm, Sherman traps, Inc., Tallahassee, FL) were set, giving 36

traps in each treatment and a total of 216 traps for this study. The traps were placed approximately 5 m apart from each other in a trapping line. The traps were placed in areas most preferred by small mammals such as next to fallen trees and boulders, next to holes in the ground and in areas with visible small mammal tracks. The location of each trapping line was recorded using a Geographic Positioning System. Additionally, each trapping line was also marked with a small wooden pole for easy location. Trapping sessions were done monthly from April to July 2006. Each trapping session lasted eight consecutive days (total = 32 trapping days). On the first day of trapping the traps were baited and set in the morning and checked in the afternoon for captures. Traps were checked every morning and afternoon thereafter for the duration of the trapping session. The traps were baited using peanut butter and oats spread on brown bread, as this makes good bait for rodents (Sutherland 1996). Pieces of apples and bananas were also added to the bait. To ensure that the animals stayed warm after capture, shredded newspaper, dried leaves and cotton wool were provided for bedding (Sutherland 1996). Captured individuals were identified and weighed to the nearest gram. Body and tail length were measured to the nearest mm using a pair of calipers. To recognize previously captured individuals each individual was marked by clipping the guard hair with a pair of sterilized scissors anywhere on the body revealing the different colored hair underneath (Sutherland 1996). The animals were then released at the point of capture and the traps were re-baited if required. Re-captured individuals were recorded as marked and released without more marking. The two similar *Mastomys* species (*Mastomys natalensis* and *Mastomys coucha*) that occur in this region were both recorded as *Mastomys spp* because they cannot be easily distinguished on qualitative external morphology (Venturi *et al.* 2004). Specimens that could not be identified to genus level were identified to species level and those that could not be identified were recorded as Unidentified 1, 2, etc. This study was conducted with the approval of the local government conservation authority Ezemvelo KZN Wildlife.

Data analysis

Using the Jolly-Seber Full Model for open populations, population size at time I (NH (I)) was estimated for each of the six treatments. This model allows for changes in population

size due to births, deaths, immigration and emigration, and is the best model for analysis in open populations (Krebs, 1999). These estimations were carried out using the Population Analysis v5 (POPAN) software programme (www.cs.umanitoba.ca/~popan/). Similarities between these areas with regard to their small mammal species composition were computed using the Bray-Curtis Coefficient on the square-root transformed data of each species in each area, from which a Rank-Similarity Matrix was constructed.

Non-metric multidimensional scaling (MDS) was then used to graphically represent the rank similarities of the treatments as points in low dimensional scale. The points that are most similar are closer to each other whereas sites that are less similar are placed further apart. The Analysis of Similarities (ANOSIM; R) was used to test for differences in small mammal assemblages between the six treatments, at 5% level of significance. Based on rank similarities between samples in the similarity matrix, $R \sim 0$ means sites are more similar to each other and $R \sim 1$ means sites are less similar to each other. These were generated using the programme Plymouth Routines In Multivariate Ecological Research (PRIMER) version 5.2 (PRIMER-E, Ltd., Plymouth, U.K.; Clarke & Warwick 2001).

To further examine the differences in small mammal assemblages between the six treatments Univariate Diversity Indices were calculated for each area using the programme PRIMER version 5. The three indices used were the Margalef's index (d), the Shannon-Wiener index (H'), and the Simpson's index (λ). They are presented as means between the sites. The Margalef's index ($d = (S - 1) / \log N$) is a measure of the number of species present for a given number of individuals (species richness) where S is the number of species and N is the total abundance per site. The Shannon- Wiener index ($H' = - \sum p_i \log (p_i)$) gives a measure of both the number of species and the equality of representation of the individuals of all species where p_i is the proportion of the total count arising from the i th species. The Simpson's index was also calculated. Both the Simpson's index ($\lambda = \sum p_i^2$), where p_i is the proportion of the total count arising from the i th species, and the Shannon-Weiner index are non-parametric measures of heterogeneity of species richness and evenness. The Simpson's index is weighted more towards the abundance of the common species while the Shannon-Weiner index places more weight on the rare species in the sample (Krebs 1999).

Trap success (Total catch x 100) / Trap nights) was calculated for each of the six areas. A trap night refers to a single trap that was set for a period of 24 hours. The Kruskal-Wallis Analysis of Variance (ANOVA; H) was applied to test for differences between the treatments using their estimated population sizes, trap success, species richness, and the diversity indices. And lastly, the Spearman's Rank Correlation (R) was applied to test for correlations between trap success, species richness and diversity between the six areas. Both these tests were conducted using the Statistica version 6 software programme (www.statsoft.com; Statsoft Inc. 2003).

Results

A total of 610 small mammals from 13 species belonging to orders Rodentia (n = 607; 12 species) and Insectivora (n = 3; two species), were captured over a total of 6912 trap nights (Table 1). The most commonly captured species (43.3 %) in all six areas was the *Mastomys spp*. The second (18.2 %) and third (12.5%) most captured species were the *Aethomys spp* and *Saccostomus campestris*, respectively, while *Petrodromus tetradactylus* was captured only once (0.16 %). The area that had never been invaded by *C. odorata* clearly had the highest estimated population size and highest trap success, while the area that had been invaded for *ca* 20 years had the lowest estimated population size and trap success (Table 1).

The MDS constructed from the similarity matrix showed that when ranked according to their similarities in species composition, the treatments appear more similar to each other (Fig. 2). However, a global ANOSIM test applied on the actual small mammal abundances showed that, generally, there were differences in small mammal assemblages between the six differing treatments (R = 0.258; p = 0.003), which indicate that there are site differences that are worth examining further. Pairs of sites were then compared and there were some significant differences between sites observed (Table 2).

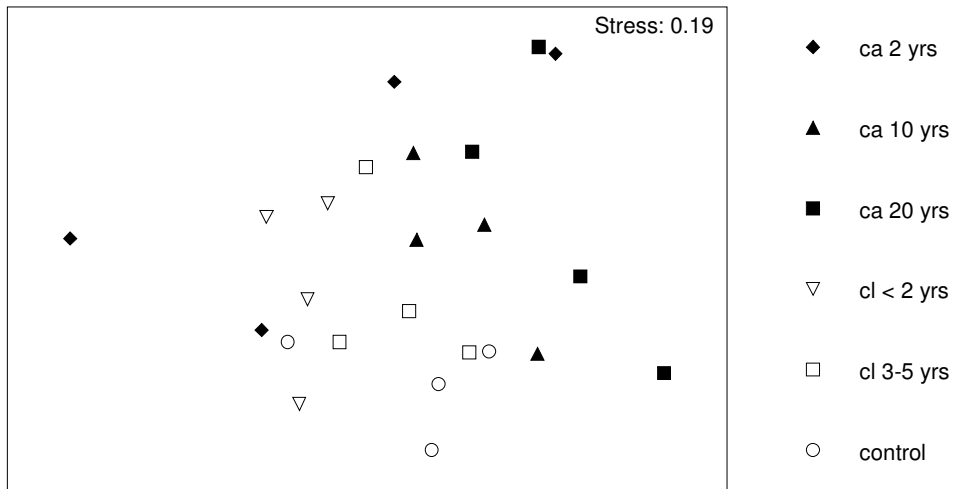


Fig. 2. MDS showing small mammal assemblages of six areas with differing *C. odorata* invasion durations, differing *C. odorata* clearing (cl) times, and a control with no *C. odorata* invasion in Hluhluwe-iMfolozi Park, South Africa.

Univariate diversity indices illustrated small differences in species richness and diversity (Fig. 3). The highest species richness and diversity were recorded in the area that had been cleared for less than two years, while the area that had been invaded for *ca* 20 years had the lowest species richness and diversity. The control area had the second highest species richness and diversity, which was still higher than any of the invaded areas, and the area that had been invaded for *ca* 2 years had higher species richness and diversity than both the area invaded for *ca* 10 years and the area invaded for *ca* 20 years (Fig. 3). Both trap success ($R = 0.83$; $p < 0.05$) and species richness ($R = 0.83$; $p < 0.05$) correlated with the Shannon-Wiener diversity index. However, the Kruskal-Wallis ANOVA showed no significant differences ($p > 0.05$) between the treatments with regard to estimated population sizes, species richness, and diversity indices.

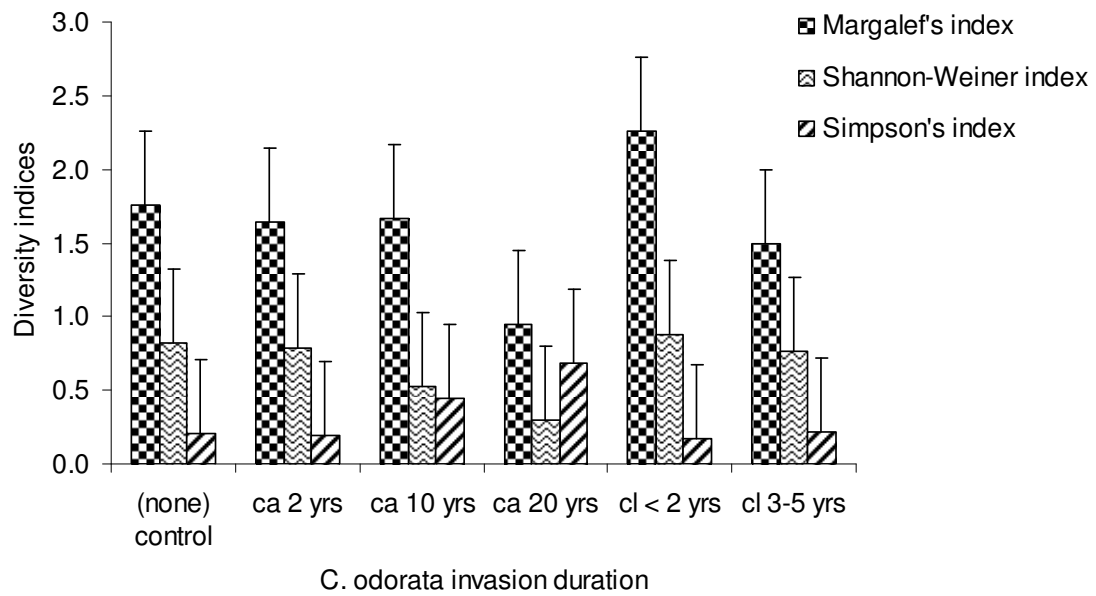


Fig. 3. Diversity indices for small mammals in six areas with differing *C. odorata* invasion durations, differing *C. odorata* clearing (cl) times, and a control with no *C. odorata* invasion in Hluhluwe-iMfolozi Park, South Africa.

Table 1: Record of the small mammal species captured in six areas with differing *C. odorata* invasion durations and differing *C. odorata* clearing times in Hluhluwe-iMfolozi Park, South Africa.

Small mammal species	<i>C. odorata</i> invasion none	<i>C. odorata</i> invasion ca 2 yrs	<i>C. odorata</i> invasion ca 10 yrs	<i>C. odorata</i> invasion ca 20 yrs	<i>C. odorata</i> clearance < 2 yrs ago	<i>C. odorata</i> clearance 3-5 yrs ago	Total individuals captured	% of total individuals captured
<i>Mastomys spp</i> (Smith 1834, 1836)	66	22	42	55	39	40	264	43.28
<i>Saccostomus campestris</i> (Peters 1846)	21	7	12	1	12	23	76	12.46
<i>Aethomys spp</i> (de Winton 1897, Thomas 1904)	17	26	5	3	45	15	111	18.20
<i>Lemniscomys rosalia</i> (Thomas 1904)	20	2	3	0	10	13	48	7.87
<i>Steatomys pratensis</i> (Peters 1846)	17	7	2	0	5	0	31	5.08
<i>Mus minutoides</i> (Smith 1834)	8	0	1	6	3	8	26	4.26
Unidentified species 1	7	0	1	0	6	5	19	3.11
<i>Tatera leucogaster</i> (Peters 1852)	12	0	0	0	0	3	15	2.46
<i>Otomys spp</i> (Wrought 1906)	0	4	0	0	7	0	11	1.80
Unidentified species 2	1	0	0	2	1	0	4	0.66
<i>Crocidura hirta</i> (Peters 1852)	0	0	0	0	2	0	2	0.33
<i>Dendromus spp</i> (Smith 1834)	0	2	0	0	0	0	2	0.33
<i>Petrodromus tetradactylus</i> (Peters 1846)	0	0	0	0	1	0	1	0.16
Total individuals captured	169	70	67	66	131	107	610	100
Observed species richness	9	7	7	5	11	7	13	-
Number of trap nights [#]	1152	1152	1152	1152	1152	1152	6912	-
Trap success (%)	14.670	6.076	5.816	5.729	11.372	9.288	-	-
Estimated population size*	113	56	62	23	70	56	-	-
Estimated survival rate*	0.467	0.578	0.651	0.659	0.558	0.465	-	-
Estimated number of births*	60.293	25.546	17.619	12.013	34.213	22.378	-	-

[#]Trap night refers to a single trap that was set for a period of 24 hours

*Calculated using POPAN 5 and the Jolly-Seber Full Model for open populations

Table 2: ANOSIM calculations for small mammal assemblages of six areas with differing *C. odorata* invasion durations, differing *C. odorata* clearing (cl) times, and a control with no *C. odorata* invasion in Hluhluwe-iMfolozi Park, South Africa.

	Test statistic (R)	Significance level (p)
ANOSIM global test between all treatments*	0.258*	0.003*
ANOSIM pairwise test between treatments		
control – ca 2 yrs	0.354	0.057
control – ca 10 yrs	0.365	0.114
control – ca 20 yrs*	0.573*	0.029*
control – cl < 2 yrs	0.281	0.114
control – cl 3-5 yrs	0.031	0.317
ca 2 yrs – ca 10 yrs	0.063	0.400
ca 2 yrs – ca 20 yrs	0.229	0.143
ca 2 yrs – cl < 2yrs	0.031	0.457
ca 2 yrs – cl 3-5 yrs*	0.354*	0.029*
ca 10 yrs – ca 20 yrs	0.052	0.343
ca 10 yrs – cl < 2 yrs	0.375	0.086
ca 10 yrs – cl 3-5 yrs	0.156	0.229
ca 20 yrs – cl < 2 yrs*	0.688*	0.029*
ca 20 yrs – cl 3-5 yrs*	0.417*	0.029*
cl < 2 yrs – cl 3-5 yrs	0.292	0.114

*Significant difference

Discussion

Although the results from this study do not show, without doubt, that differences in small mammal species richness and diversity between the treatments were due to the invasion by *C. odorata*, due to lack of statistical significance, we can speculate that invasion by *C. odorata* contributed in these differences and more research on this would prove the point. It needs to be kept in mind that findings do not necessarily need to be statistically significant to be biologically significant. The results from this study that suggest that the changes in species richness and diversity were due to the invasion by *C. odorata*, although not statistically significant, are discussed below.

The marked dominance of *Mastomys spp* in the invaded areas is an indication of disturbed habitat as this species dominates most disturbed habitats (Avenant & Kuyler 2002). The results show that *Mastomys spp* also rapidly colonize areas that have been disturbed by alien plant invasions. Many studies have reported *Mastomys spp* as highly opportunistic species (e.g. Ferreira & van Aarde 1996; Monadjem 1997; Avenant 2000) because they tolerate disturbance well and have generalized ecological requirements (Fuller & Perrin 2001). They are often the first colonizers after disturbances like fire, drought, overgrazing and cultivation (Rowe-Rowe 1995).

Results from the population size estimates show that the control area had the highest estimated population size, which was almost four times that found in the area that had been invaded for *ca* 20 years, suggesting a decrease in preference of habitats by small mammals with the increase in invasion duration. Both population size and trap success decreased with the increase in *C. odorata* invasion duration. This suggests a decrease in preference of the habitats with the increase in invasion duration. This could be attributed to the lack of vegetation cover suitable for small mammals in areas invaded by *C. odorata*.

Although the MDS showed some similarity in sites (Fig. 2), the ANOSIM test results showed significant differences between some pairwise groups of the treatments (Table 1). Of the three sample areas with varying *C. odorata* invasion duration (*ca* 2 yrs, *ca* 10 yrs, *ca* 20 yrs), only the area invaded for the longest period showed significant differences in small mammal assemblages when compared to the control area ($R = 0.573$; $p = 0.029$). This suggests that, although small mammal species are negatively affected by *C. odorata*

invasion, a statistically significant effect on species richness and diversity only becomes visible with the persistence of the invasion. It is therefore important to note that sampling small mammals in areas with different invasion durations is crucial, as otherwise, if only the areas invaded between two and 10 years had been sampled, the conclusion that *C. odorata* invasions have little effect on small mammal species richness and diversity would have been drawn. However, it needs to be kept in mind that findings do not necessarily need to be statistically significant to be biologically significant.

We were unable to find any studies that have quantified the effects of invasive plants on native fauna with regard to the duration of the invasions. However, Strayer *et al.* (2006) suggest that the effects of many invaders change over time. They continue by suggesting that invasions generally have an acute phase immediately after a new invasion, followed by a chronic phase after various ecological processes have occurred. This statement is supported by results from this study, as there is a marked decrease in small mammal diversity (Fig. 3), estimated population size, trap success and the number of estimated number of births entering the community (Table 1), with increase in invasion duration. This suggests that the more time the invader is left to establish, the more the habitat is disturbed and the more species are lost.

Vegetation cover and food availability are important aspects for the well being of small mammals. Monadjem (1997) found a positive correlation between small mammal diversity and vegetation density in Swaziland grassland. It has been found that *C. odorata* has had a considerably toxic effect on indigenous vegetation (MacDonald 1983), which is likely to affect food quality and availability of suitable habitat for small mammals. Hence, the observed decrease in small mammal species richness and diversity with increasing invasion duration can most likely be attributed to, for the small mammals, negative effect of *C. odorata* on vegetation and food.

Significant differences in small mammal assemblages were observed between the area that had been invaded for *ca* 20 years and both cleared areas (i.e. cl < 2 yrs and cl 3-5 yrs) as well as between the recently invaded area (*ca* 2 yrs) and the area that had been cleared for 3-5 years. This is evidence that clearing of *C. odorata* results in restoration of the native communities and thus the ecosystem. Many studies have shown that removal of alien invasive plants result in the recovery of native communities, indicating the

rehabilitation of the ecosystem. Samways *et al.* (2005), for example, reported on the recovery of three species of Odonata that were feared to be extinct, but that reappeared after removal of alien invasive plants. Gratton & Denno (2005) observed rapid recovery of arthropod assemblages due to the re-establishment of *Spartina alterniflora* marshes following the removal of the invasive wetland plant *Phragmites australis*. It was expected that areas that had been cleared for a longer period, 3-5 years in this case, would have higher species richness and diversity than areas that had recently been cleared (< 2 yrs). However, the results of this study did not support this. The reason could be that there was no follow-up work done after the initial clearing. Lack of follow-up work has been known to result in re-invasion of the cleared areas by *C. odorata* (MacDonald 1983).

It was also expected that the area that had never been invaded would have the highest species richness and diversity, but the area that had recently been cleared (< 2 yrs) had the highest species richness and diversity (Fig. 3). The reasons for this are not clear, but could be attributed to the fact that the area had been unsuitable for small mammals for a long time due to *C. odorata* invasions and recolonisation was taking place from adjacent areas after removal of *C. odorata*, but this is subject to further investigations. Following natural disturbance is a process of vegetational succession of habitats. It has been shown that changes in small mammal communities during vegetation succession are correlated with changes in vegetation composition and structure (Fox 1990). Therefore, although not measured in this study, the vegetational succession following removal of alien plants may have resulted to the high small mammal diversity in the recently (< 2 years) cleared area.

Conclusions

The rising disappearance and degradation of natural environments have increased the need to conserve and restore biological diversity, and alien plant invasions are proving to be one of the biggest threats to biodiversity worldwide. In South Africa, *C. odorata* is amongst the most problematic alien plant species that needs prioritisation. It is the most widespread alien plant in Hluhluwe-iMfolozi Park, which is situated in the Maputaland centre of endemism, one of the biodiversity hotspots of South Africa. This alien invasive

plant poses a serious threat to the long-term maintenance of natural vegetation within the area and has invaded virtually all the protected areas in this region. Understanding the effects of invasive plants on many, if not all, levels of biodiversity is important in order to make sound decisions regarding the eradication of such plants. This study shows deleterious effects in small mammal communities resulting from *C. odorata* invasion, thereby indicating an unhealthy ecosystem. It is further shown that clearing of this plant results in rehabilitation of the ecosystem, however, follow-up clearing is shown to be absolutely essential for the successful re-establishment of the native flora and fauna, as cleared areas become re-invaded with the corresponding negative effects within a period of three to five years after first clearing. We conclude that managers of conservation areas should prioritize the removal of alien invasive plants as well as the maintenance of cleared sites in order to maintain healthy native ecosystems.

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CHAPTER 3

The effects of an alien invasive plant (*Chromolaena odorata*) on large mammal diversity

Abstract

Invasion by exotic species (plants and animals) has been rated as the second largest threat to global biodiversity after habitat destruction. Alien plants have invaded most ecosystem types (terrestrial, fresh water and marine) and are responsible for loss of irreplaceable natural services on which human kind relies. They alter food quantity, quality and accessibility, and may result to declines in native species richness, which may ultimately result into extinction. For the effective management of invasive alien plants, it is important to understand the effects that such plants have on all levels of biodiversity. However, the effects that invasive alien plants, such as the Triffid weed (*Chromolaena odorata*), have on mammalian biodiversity, especially large mammalian species are not well known, although they play major ecological roles in areas such as nutrient cycling. Also, a little is known about the recovery of the ecosystem following alien plant removal. This study investigated the effects of *C. odorata* invasions on large mammalian herbivores in Hluhluwe-iMfolozi Park and whether clearing of this plant helped in rehabilitating the habitat. We used track counts to estimate and compare species richness, diversity and abundance indices for large mammalian species between areas with differing *C. odorata* invasion durations (*ca* 2 years, *ca* 10 years, *ca* 20 years), areas with differing clearing times (cl < 2 years, cl 3-5 years) and an area with no history of *C. odorata* invasion as a control. We found significant differences between communities and diversity between treatments, showing a negative effect of the invasive but also a positive effect of clearing.

Introduction

Biotic invasions are altering the world's natural communities and their ecological character at an extraordinarily rapid rate (Mack *et al.* 2000). Invasion by exotic species is therefore rated as the second largest threat to global biodiversity, after habitat destruction (Schei 1996). Invasive alien plants have invaded most ecosystem types (terrestrial, fresh water and marine) (Williamson 1999) as well as areas used for agriculture (Sharma *et al.* 2005). The impacts of biotic invasions on the ecosystem are numerous and vary a great deal (Mack *et al.* 2000). Basic ecological properties of ecosystems may be changed (Vitousek 1990) and native plant dynamics and animal species population biology may be altered (Sakai *et al.* 2001), resulting in homogenization of the ecosystem (McKinney & Lockwood 1999) and/or loss of irreplaceable natural services on which human kind relies (Mack *et al.* 2000). For example, food webs may be affected in such a manner that the quantity and/or quality of food is altered, thus changing food accessibility and vulnerability to predators (Zedler & Kercher 2004). Also, native plant and animal species may be reduced or displaced (Schofield 1989), thereby altering the physical characteristics of the invaded habitats (Gratton & Denno 2005). Several authors have found that native species, which co-exist with an invasive plant in the standing vegetation, may suffer a reduction in productivity due to competitive interaction with the invader (Walck *et al.* 1999; Gould & Gorchov 2000; Miller & Gorchov 2004) and declines in native species richness have been demonstrated in a variety of communities following invasion (D'Antonio & Vitousek 1992).

Triffid weed *Chromolaena odorata* (L.) R.M. King and H. Robinson (*Asteraceae*) is an invasive plant that is native to the Neotropics and that occurs in suitable areas below an altitude of 1000 m. It is a plant of secondary succession with an extensive fibrous root system that is capable of rapidly invading clearings where it forms tangled bushes and may reach a height of six meters as a scrambler up trees (McFadyen & Skarratt 1996). *C. odorata* is highly flammable and burns even when green (MacDonald 1983) and has the potential to out-compete indigenous vegetation through allelopathy (Fitter 2003). First recorded in South Africa in the mid 1940s, *C. odorata* has reached alarming proportions, making it one of the worst weeds in the southern African subregion (Goodall & Erasmus 1996). In KwaZulu-Natal, where it is the most widespread invasive plant, it has invaded

virtually all conservation areas and, indeed, in HiP, it poses the greatest threat to the natural vegetation (Macdonald 1983).

For the effective control of invasive alien plants, it is vital that the effects of such species on native communities be recognised. Leslie & Spotila (2001) for example found that *C. odorata* invasions had a shading effect on nesting sites of a keystone species in the Greater St. Lucia Wetland Park (GSLWP), KwaZulu-Natal, the Nile crocodile (*Crocodylus niloticus*), thus posing a serious threat to its continued survival. Samways & Taylor (2004) found that alien invasive plants pose a great threat to the survival of the Red-listed South African dragonflies (Odonata), as they destroy the dragonflies' habitats by shading the subcanopy vegetation and thereby making conditions too dark for the dragonflies. More recently, Valtonen *et al.* (2006) found that, in Finland, invasions by the lupine plant (*Lupinus polyphyllus*) decreased the cover and species richness of potential host plants for larvae and nectar plants for adult Lepidoptera butterflies.

However, the effects of alien plant invasions on mammalian species, especially large species, are not well documented. Large mammalian herbivores are characteristic parts of the world's ecosystems due to their major ecological roles in areas such as nutrient cycling (Holland & Detling 1990; McNaughton *et al.* 1997) and determination of vegetation structure and composition (Augustine & McNaughton 1998), which ultimately affect the abundance and diversity of most other taxa (Milchunas *et al.* 1998). It is therefore important that factors that affect large mammalian populations be recognised.

Large mammalian species select their habitats according to the habitats' ability to provide food, water, shelter from climatic extremes and protection from predators, which are the four factors required for their survival (Sinclair 1977). Any disturbances to the habitat that result in them lacking one or all of these factors affect large mammalian populations. Disturbance of large mammalian species habitats result from activities such as forest logging (Wilson & Johns 1982), selective logging of plantations (Heydon & Bulloh 1997), intense hunting pressure (Lopes & Ferrari 2000; Laurance *et al.* 2006) road constructions that run through areas inhabited by mammalian species (Laurance *et al.* 2006). Clearing of forests for agricultural purposes has resulted in changes in forest composition, which has impacted large mammalian species inhabiting these forests, as the secondary vegetation that comes after these clearings might not provide sufficient food

items (Wilkie & Finn 1990). One of the greatest threats to large mammalian habitats, as is to all other habitats, is the invasion by alien plant species. Alien invasive plants such as *C. odorata* change the structure of the habitat by outcompeting native plant species through their allelopathic characteristics (Zachariades & Goodall 2002), thus affecting other levels of taxa.

It is important that the effects that such plants have on all levels of biodiversity be recognised for their effective control, which has become an important conservation focus (Wittenberg & Cock 2005). The control of invasive species, which reduces the presence of the invader, together with the eradication of alien invasive plants to restore natural habitats is becoming an important tool in the management of natural resources and ecosystem functioning (Weinstein *et al.* 1997). However, there is not much knowledge on whether the ecosystem recovers after the removal of invasive alien species. In the context of the above, this study documents the effects of the invasive alien plant *C. odorata* on the diversity of large mammalian species and assesses whether the clearing of this plant helps in the recovery of the natural vegetation in Hluhluwe-iMfolozi Park. The current study aims to document the effects of *C. odorata* invasions have on the use of habitat by large mammal species in HiP, by determining the differences in diversity and abundance of large mammalian species between invaded and uninvaded areas.

Methods

Study area

This study was conducted in Hluhluwe-iMfolozi Park (HiP), a protected natural area located in central KwaZulu-Natal. HiP lies between latitudes 28° 00' to 28° 26' S and longitudes 31° 43' to 32° 09' E. It covers an area of approximately 960 km² and is comprised of the 300 km² Hluhluwe section in the north and the 660 km² iMfolozi section in the south. The vegetation is predominantly savanna woodlands with some evergreen forests and grasslands (Whateley & Porter 1983).

HiP has a diverse mammal fauna, which include all the African megaherbivores: the African elephant (*Loxodonta africana*), the black rhinoceros (*Diceros bicornis*), the white rhinoceros (*Ceratotherium simum*), the hippopotamus (*Hippopotamus amphibius*), and giraffe (*Giraffa camelopardalis*), as well as a wide spectrum of other herbivores,

carnivores, small mammals and other taxa. This study was conducted in the Hluhluwe section of the Park where most *C. odorata* invasions have occurred.

Site selection

Using historical maps of the distribution of *C. odorata* in the Park (provided by Ezemvelo KZN Wildlife), six treatments with differing *C. odorata* invasion durations and differing clearing times were selected. These treatments included one that had recently been invaded (*ca* 2 years); two that had been invaded for a longer period (*ca* 10 years and *ca* 20 years); a treatment that had recently been cleared (*cl* <2 years); a treatment that had been cleared for a longer period (*cl* 3-5 years); and finally, as a control, a treatment that had no history of *C. odorata* invasion. The treatments were located in a section of the park dominated by the white Stinkwood tree (*Celtis Africana*) and were very similar in vegetation composition, but differed in *C. odorata* invasion duration and clearing times.

Tracking plots

We used tracking plots to estimate large mammalian species richness and diversity and abundance. In each of the six treatments tracking plots were created along tracks that showed evidence of mammalian utilisation. Tracking plots were replicated eight times in each treatment, totalling 48 plots for the study. Located approximately 100 meters apart and in different stands of *C. odorata*, each plot was created by removing vegetation in a space three metres long and one metre wide. The plots were raked and smoothed and fine soil, of the same type as in the vicinity, was added to provide a good tracking surface and to ensure that the animals could not visually distinguish the plots from their usual road track. Using a Global Positioning System unit the position of each tracking plot was recorded. All tracking plots were examined for tracks at least twice a week from February to June 2006, making a total of 27 tracking days. At each tracking plot, the number of track sets left by each mammal species were recorded, after which the plots were raked and smoothed in preparation for the following observation (e.g. Wilkie & Finn 1990; Engeman & Allen 2000; Engeman & Evangelista 2006). To avoid pseudo-replication, an attempt was made to determine whether track sets belonged to the same animal that, maybe, wondered around the plot or walked across the tracking plot or to different animals.

Data analysis

The mean number of tracks recorded for each species in each treatment site per day was calculated as a relative index of species abundance (Wilkie & Finn 1990). This was then compared between the different treatments. The data were square root transformed to down-weight the importance of the highly abundant species, and using the Bray-Curtis coefficient, similarities between samples were computed and a rank-similarity matrix was constructed. From the rank-similarity matrix, a non-metric multidimensional scaling (nMDS) was constructed to graphically represent the samples as points in low-dimensional scale. Each tracking plot was treated as one sample. Thus, there were eight samples in each treatment and a total of 48 samples throughout the study area. The nMDS plots samples that are similar in their species composition closer together, and samples that differ in species composition are plotted further apart in a two-dimensional ordination space.

An Analysis of Similarities (ANOSIM; R) was used to test for significant differences in the animal species composition of the treatments. The ANOSIM tests the hypothesis of no differences between sites, using the rank similarities between samples. The test statistic R gives a measure of the degree of similarity between sites, with $R \sim 1$ indicating that treatments were very different in species composition and $R \sim 0$ indicating that treatments were more similar in species compositions. A global ANOSIM test was used to give an indication of whether there were, generally, differences between the treatments; and pairwise tests between the treatments examined the differences in rank similarities of the sites, at 5% level of significance.

To further examine the differences in mammal species composition between the treatments, univariate diversity indices were calculated. These were the Shannon Weiner and the Simpson's indices, which give measures of heterogeneity of species richness and evenness (where the Shannon Weiner index places more weight on the abundance of rarer species, while the Simpson's index is weighted more towards the abundance of the common species) (Krebs 1999). All these calculations were carried out using the PRIMER v5 software (PRIMER-E, Ltd., Plymouth, U.K.; Clarke & Warwick 2001). The Kruskal-Wallis test ANOVA (H) was used to test for differences between the treatments using the diversity indices and the relative indices of abundances, at 5% level of significance.

Results

A total of 3469 tracks from 17 large mammalian species were recorded during the study period. The majority of recorded tracks belonged to the family Bovidae and the most commonly recorded species were nyala (*Tragelaphus angasii*), impala (*Aepyceros melampus*) and African buffalo (*Syncerus caffer*), which accounted for 42.4%, 14.9% and 11.1% of the total number of tracks recorded, respectively (Table 3). The most tracks were recorded in the treatment that had never been invaded with *C. odorata* (19.9%) while the treatment invaded for *ca* 20 years displayed the lowest number of tracks (10.5%) (Table 3). Of all recorded species, the African buffalo was the only species that did not occur in any of the invaded treatments (*ca* 2 years, *ca* 10 years and *ca* 20 years); the highest number of African buffalo tracks was recorded in the treatment that had recently been cleared (*cl* <2 years). The tracks of the only two recorded carnivores, lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*), were only found in the treatments that had been invaded for *ca* 20 years and *ca* 10 years, respectively.

The Kruskal-Wallis ANOVA test showed a significant differences between the treatments with regard to the diversity indices ($p > 0.05$) (Fig. 4), with a pairwise comparison showing that the *ca* 5 & 10 years invaded treatments were significantly different to the control (Table 4). The treatment that had never been invaded had the highest diversity indices in comparison to the three invaded treatments (Fig. 4). Also, diversity decreased with the increase in invasion duration, with the treatment that had been invaded for *ca* 20 years displaying the lowest species richness and diversity. The recently invaded treatment (*ca* 2 years) had higher diversity indices than both treatments that had been invaded for a longer period (*ca* 10 years and *ca* 20 years) (Fig. 4). Both cleared treatments (*cl* < 2 years and *cl* 3-5 years) had a higher diversity than the treatment that had been invaded for *ca* 20 years. The treatment that had been cleared for a longer period (*cl* 3-5 years) had a higher species richness than all the invaded treatments and a higher diversity than both treatments that had been invaded for a longer period (*ca* 10 years and *ca* 20 years) (Fig. 4).

Table 3: Total number of tracks recorded per large mammal species in areas with differing *C. odorata* invasion and clearing (cl) times and in a control area with no history of *C. odorata* invasion in Hluhluwe-iMfolozi Park

Large mammal species recorded	Common name	<i>C. odorata</i> invasion none	<i>C. odorata</i> invasion ca 2yrs	<i>C. odorata</i> invasion ca 10yrs	<i>C. odorata</i> invasion ca 20yrs	<i>C. odorata</i> clearance <2yrs	<i>C. odorata</i> clearance 3-5yrs	Total individuals recorded	% of total individuals recorded
Bovidae									
<i>Aepyceros melampus</i>	Impala	116	110	91	0	72	131	520	15.0
<i>Cephalophus natalensis</i>	Red duiker	25	44	21	25	27	32	174	5.0
<i>Connochaetes taurinus</i>	Blue wildebeest	5	33	0	0	37	18	93	2.7
<i>Kobus ellipsiprymnus</i>	Waterbuck	43	0	0	46	0	0	89	2.6
<i>Redunca spp</i>	Reedbuck	13	5	17	10	0	9	54	1.6
<i>Syncerus caffer</i>	African buffalo	76	0	0	0	277	33	386	11.1
<i>Tragelaphus angasii</i>	Nyala	247	244	269	223	169	319	1471	42.4
<i>Tragelaphus strepsiceros</i>	Greater kudu	18	32	0	0	0	32	82	2.4
Cercopithecidae									
<i>Papio hamadryas</i>	Chacma baboon	16	0	26	0	0	3	45	1.3
Elephantidae									
<i>Loxodonta africana</i>	African elephant	19	14	18	19	11	0	81	2.3
Equidae									
<i>Equus quagga</i>	Plains Zebra	7	71	16	0	23	31	148	4.3
Felidae									
<i>Panthera leo</i>	Lion	0	0	0	2	0	0	2	0.1
Giraffidae									
<i>Giraffa camelopardalis</i>	Giraffe	27	9	0	0	0	26	62	1.8
Hippopotamidae									
<i>Hippopotamus amphibius</i>	Hippopotamus	4	0	5	5	0	0	14	0.4

Hyaenidae									
<i>Crocuta crocuta</i>	Spotted hyaena	0	0	2	0	0	0	2	0.1
Rhinocerotidae									
<i>Ceratotherium simum</i>	White rhinoceros	28	0	4	0	14	0	46	1.3
Suidae									
<i>Phacochoerus africanus</i>	Warthog	47	33	18	35	36	31	200	5.8
Total no. of tracks		691	595	487	365	666	665	3469	100
Total no. of species		15	10	11	8	9	11		

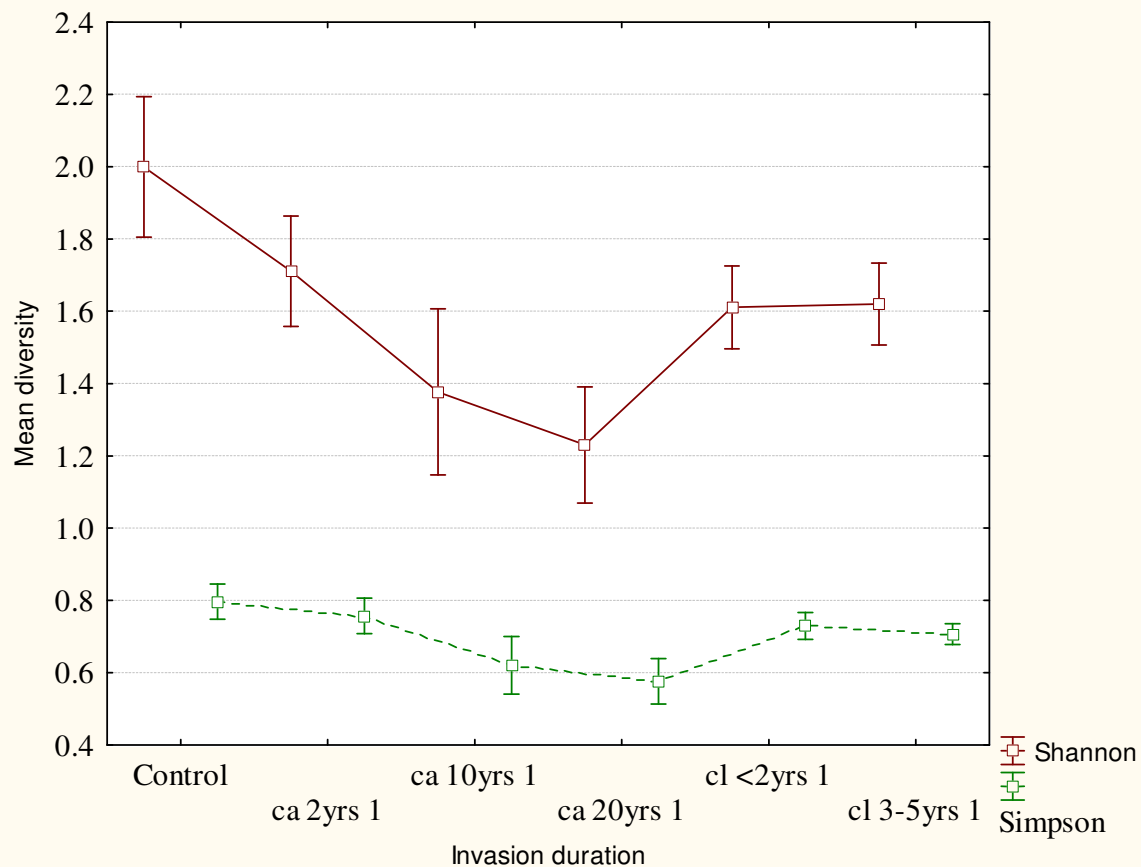


Fig. 4. Mean diversity (\pm 95% confidence limits) of mammals from areas with differing *C. odorata* invasion durations, differing *C. odorata* clearing (cl) times, and in a control area with no history of *C. odorata* invasion in Hluhluwe-iMfolozi Park, South Africa.

The nMDS shows that, when grouped according to rank similarities, samples from the same treatment are more similar to each other than to any other sites from other treatments. This means that there are differences in animal species composition between the selected treatments (Fig.5). Sites from the treatment that had been invaded for *ca* 20 years are plotted with the greatest distance from all other sites. Sites from the treatment that had been cleared for a longer time (cl 3-5 years) appear closer to sites from the treatment that had recently been invaded (*ca* 2 years) on the nMDS, suggesting some similarities in

mammal species composition between these treatments. All six treatments were different in species composition (Global ANOSIM, $R = 0.946$, $p = 0.001$; pairwise ANOSIM. Table 5). The pairwise ANOSIM test statistic R -values were all close to one (Table 5), suggesting that similarities between samples from one treatment are much less than any similarities between samples from other treatments. Based on this, the hypothesis of no differences is then rejected.

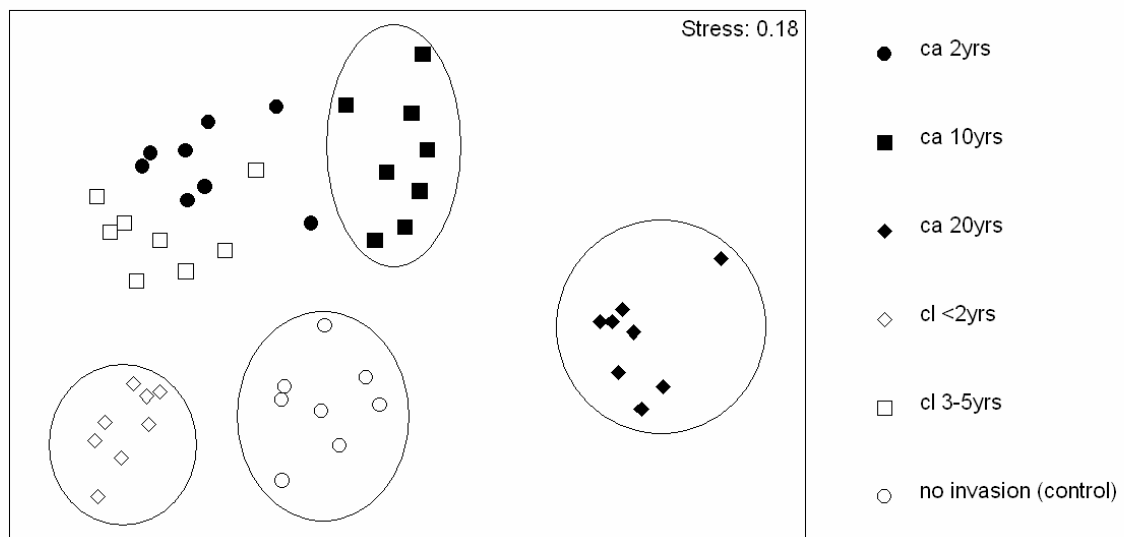


Fig. 5. nMDS showing large mammal species assemblages in areas with differing *C. odorata* invasion durations, differing *C. odorata* clearing (cl) times, and in a control area with no history of *C. odorata* invasion in Hluhluwe-iMfolozi Park, South Africa.

There was no significant ($p > 0.05$) difference between the indices of relative abundances for all species (Table 6). The three most commonly recorded species (nyala, impala and African buffalo) had the highest relative abundances in the cleared treatments, with the nyala and impala most abundant in the treatment that had been cleared for a longer time (cl 3-5 years) and the African buffalo most abundant in the treatment that had recently been cleared (cl < 2 years) (Table 6).

Table 4: Multiple Comparisons *P* values (2-tailed) of Simpson and Shannon diversity indices. Significant values ($p < 0.05$) are indicated in bold.

	Control	<i>ca</i> 2yrs	<i>ca</i> 10yrs	<i>ca</i> 20yrs	<i>cl</i> < 2yrs	<i>cl</i> 3-5yrs
Simpson						
Control		1.0000	0.0046	0.0003	1.0000	0.3840
<i>ca</i> 2yrs	1.0000		0.0606	0.0065	1.0000	1.0000
<i>ca</i> 10yrs	0.0046	0.0606		1.0000	0.6825	1.0000
<i>ca</i> 20yrs	0.0003	0.0065	1.0000		0.1233	0.6540
<i>cl</i> < 2yrs	1.0000	1.0000	0.6825	0.1233		1.0000
<i>cl</i> 3-5yrs	0.3840	1.0000	1.0000	0.6540	1.0000	
Shannon						
Control		1.0000	0.0017	0.0001	0.2898	0.3039
<i>ca</i> 2yrs	1.0000		0.2507	0.0184	1.0000	1.0000
<i>ca</i> 10yrs	0.0017	0.2507		1.0000	1.0000	1.0000
<i>ca</i> 20yrs	0.0001	0.0184	1.0000		0.2762	0.2632
<i>cl</i> < 2yrs	0.2898	1.0000	1.0000	0.2762		1.0000
<i>cl</i> 3-5yrs	0.3039	1.0000	1.0000	0.2632	1.0000	

Table 5: ANOSIM results showing significant differences in large mammal composition in areas with differing *C. odorata* invasion and clearing (cl) times and in a control area with no history of *C. odorata* invasion in Hluhluwe-iMfolozi Park. Global R = 0.946; p = 0.001.

Pairwise groups	Statistic (R)	Level of significance (p)
control, ca 2yrs	0.994	0.001
control, ca 10yrs	0.935	0.001
control, ca 20yrs	0.997	0.001
control, cl < 2yrs	1	0.001
control, cl 3-5yrs	0.938	0.001
ca 2yrs, ca 10yrs	0.876	0.001
ca 2yrs, ca 20yrs	0.999	0.001
ca 2yrs, cl < 2yrs	0.965	0.001
ca 2yrs, cl 3-5yrs	0.529	0.001
ca 10yrs, ca 20yrs	0.989	0.001
ca 10yrs, cl < 2yrs	0.993	0.001
ca 10yrs, cl 3-5yrs	0.947	0.002
ca 20yrs, cl < 2yrs	1	0.001
ca 20yrs, cl 3-5yrs	1	0.001
cl < 2yrs, cl 3-5yrs	0.999	0.001

Table 6: Relative index of abundance for each large mammal species recorded in areas with differing *C. odorata* invasion, differing clearing (cl) time and in a control area with no history of *C. odorata* invasion in Hluhluwe-iMfolozi Park.

Species	Common name	No invasion	ca 2yrs	ca 10yrs	ca 20yrs	cl <2yrs	cl 3-5yrs
Bovidae							
<i>Aepyceros melampus</i>	Impala	4.296	4.074	3.37	0	2.667	4.852
<i>Cephalos natalensis</i>	Red duiker	0.926	1.63	0.778	0.926	1	1.185
<i>Connochaetes taurinus</i>	Blue wildebeest	0.185	1.222	0	0	1.37	0.667
<i>Kobus ellipsiprymnus</i>	Waterbuck	1.593	0	0	1.704	0	0
<i>Redunca arundinum</i>	Reedbuck	0.481	0.185	0.63	0.37	0	0.333
<i>Syncerus caffer</i>	African buffalo	2.815	0	0	0	10.259	1.222
<i>Tragelaphus angasii</i>	Nyala	9.148	9.037	9.963	8.259	6.259	11.815
<i>Tragelaphus strepsiceros</i>	Kudu	0.667	1.185	0	0	0	1.185
Cercopithecidae							
<i>Papio ursinus</i>	Baboon	0.593	0	0.963	0	0	0.111
Elephantidae							
<i>Loxodonta africana</i>	Elephant	0.704	0.519	0.667	0.704	0.407	0
Equidae							
<i>Equus quagga</i>	Zebra	0.259	2.63	0.593	0	0.852	1.148
Felidae							
<i>Panthera leo</i>	Lion	0	0	0	0.074	0	0
Giraffidae							
<i>Giraffa camelopardalis</i>	Giraffe	1	0.333	0	0	0	0.963
Hippopotamidae							
<i>Hippopotamus amphibius</i>	Hippo	0.148	0	0.185	0.185	0	0
Hyaenidae							
<i>Crocuta crocuta</i>	Hyaena	0	0	0.074	0	0	0
Rhinocerotidae							
<i>Ceratotherium simum</i>	White rhino	1.037	0	0.148	0	0.519	0
Suidae							
<i>Phacochoerus africanus</i>	Warthog	1.741	1.222	0.667	1.296	1.333	1.148

Discussion

Our data shows that *C. odorata* invasions have a negative affect large on mammal communities. We show mammalian species richness and diversity is highest in the control treatment after which it decreases with increasing *C. odorata* invasion duration, with the treatment that had been invaded for the longest time (*ca* 20 years) displaying the lowest number of species. This suggests that the longer this invasive plant is left to establish, the less preferable the habitat becomes to large mammals. These finding are supported by a multitude of studies which have found invasive plants to have a devastating influence native organisms (although mostly plants) and pose a threat to diversity (Richardson, Williams & Hobbs 1994; Pyšek & Pyšek 1995; Cole & Landres 1996).

Our data also clearly shows that samples from similar treatments are more similar to each other in mammalian species composition than to samples from other treatments, showing that there are differences in species composition between the six treatments. As the nMDS groups samples that are similar close together, the fact that samples from the treatment that had been invaded for *ca* 20 years are plotted the farthest away from all other samples shows that this treatment displays the most different mammalian species composition in comparison to the other treatments. This clearly highlights the long-term impact of *C. odorata*. This is supported by sites from the treatments that had been cleared for 3-5 years which appeared to have similar species composition to that from sites in the treatments that had been invaded for *ca* 2 years. This suggests that, despite the treatments having the same vegetation type, they differ in species composition, which in turn could be attributed to the presence of *C. odorata*.

The abundance of certain species, such as impala, nyala, red duiker (*Cephalophus natalensis*) and warthog (*Phacochoerus africanus*), is very similar in invaded and un-invaded treatments, suggesting either indifference to or even preference for these treatments. We suggest that these species use *C. odorata* invaded areas to hide from predators, as most of these species fall prey to a number of carnivores. As nyala are associated with thickets (Skinner & Chimimba 2005), *C. odorata* could also be providing suitable habitat for shelter and not only space to hide. No buffalo tracks were recorded in any of the invaded treatments which indicate that, although they could provide shelter, these areas were not suitable habitat. Although buffalo are regarded as unselective bulk

grazers (Sinclair 1977), they have been found to adjust their selection of grass species and feeding localities in relation to seasonal changes which change the quantity and quality of food (Macandza, Owen-Smith & Cross 2004). They are therefore probably just using alternative more suitable habitats. Lion and spotted hyaena tracks were only recorded in densely invaded treatment (*ca* 10 years and *ca* 20 years), which could be attributed to lions selecting areas where prey would be easier to catch (Hopcraft, Sinclair & Packer 2005).

Our results suggest that *C. odorata* invasions change the habitat for use by large mammals either by outcompeting native plant species through their allelopathic characteristics (Zachariades & Goodall 2002), shading, competition for moisture, or nutrients. Although diversity improves with clearing, species composition remains different to pre-invasion state. This is concerning as it therefore appears that the habitat may remain changed for a long time after clearing. *Chromolaena odorata* has also been found to have negative effects on some of the high-profile species in South Africa, such as the Nile crocodile in the GSLWP (Leslie & Spotila 2001) and possibly the black rhinoceros in HiP (Reid *et al.* 2007). We suggest that if *C. odorata* is affecting large organisms then they will be having an even greater affect on smaller taxa, both directly through habitat change and indirectly through the affects of the changed ungulate community.

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CHAPTER 4

Conclusions

In the present study the effects of *C. odorata* on small and large mammal diversity were investigated and it was found that *C. odorata* invasions resulted in reduced small and large mammal species richness and diversity, as it disturbs their habitats and reduces food availability. Because shelter, food, water and safety from predators are the key requirements for mammal survival, the reduced species richness and diversity in *C. odorata* invaded areas suggests that these areas either lack one or all of these factors. The present study has also shown that the more time this invasive plant is left to establish, the more destructive it becomes to the habitat, as the species richness of both small and large mammals decreased with the increase in *C. odorata* invasion duration. It is therefore important to note that the effects of invasive alien plants on mammals worsen with time, thus showing the need to control, or eradicate when possible, such plants. By out-competing native plant species, invasive alien plants result in habitat destruction, which in turn affects most of the native faunal diversity, including mammals. Because they tend to take over the habitats that they invade, invasive alien plants result in the reduction of most plant species richness and diversity, some of which have specialist animal predators thus affecting the species richness and diversity of such animals by reducing the availability of resources required for survival.

This study has also shown that removal of invasive alien plants does help in rehabilitation of the ecosystem, as both small mammal species richness and large mammal abundance and species richness increased in the areas cleared of *C. odorata*. Very little is known about the recovery of biodiversity after the removal of alien invasive plants (Samways, Taylor & Tarboton 2005). A few studies have shown that alien plant removal facilitates ecosystem recovery (e.g. Samways *et al.* 2005; Gratton & Denno 2005). This study, therefore, has shown that the control of *C. odorata* by way of cutting and application of herbicides does help the ecosystem to recover. However, it is important that the process of controlling this plant be continuous as lack of follow-up work on cleared areas results in reinvasions which negatively affects native fauna.

HiP is known for its highly maintained natural vegetation and one of the main objectives of its management is to maintain viable populations of as many indigenous species in the park as possible (MacDonald 1983). However, bush encroachment (Skowno *et al.* 1999; Bond, Smythe & Balfour 2001) together with invasions by alien plant species, which *C. odorata* is the most widespread, have been obstacles in the accomplishment of this objective (Macdonald 1983). *C. odorata* has invaded most nature conservation areas in KwaZulu-Natal (MacDonald 1983) and is ranked as the second most problematic alien plant in South Africa (Robertson *et al.* 2003). Because of its allelopathic characteristics, that allow it to outcompete indigenous plants (Zachariades & Goodall 2002), *C. odorata* invasions result in changes in all indigenous taxa. Control of such plants as *C. odorata* has become one of the important tools in managing natural resources and documenting the effects that they have on other levels of biodiversity is essential for the effectiveness of their control.

Invasions by alien species have resulted to degradation of natural habitats and this has amplified the need to conserve biological diversity (Gratton & Denno 2005). Most ecosystem types have, to some extent, been invaded by alien plants (Williamson 1999). South Africa has been deemed as having the highest known concentration of threatened plants and the highest extinction estimates for any other country in the world (Wynberg 2002). Invasions by problem plants such as *C. odorata* maybe responsible for further extinctions. *C. odorata* is known to reduce grassland, savanna and forest vegetations to monotypic vegetations (Goodall & Zachariades 2002). It is therefore important that prevention, control and eradication of alien species be prioritised by managers of conservation areas in order to reduce or prevent loss of native species.

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