The ideal weed?

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Introduction

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Biological invasions

In the last centuries biological invasions have become an important global phenomenon and constitute one of the most serious threats to biodiversity worldwide (Lonsdale 1999). Invasions are characterized by the proliferation, spread and persistence of species in new areas that are often very distant from their native ranges (Mack et al. 2000). They largely result from the ever-expanding human transport and commerce that deliberately or accidentally distribute species around the face of the earth, moving them beyond their natural dispersal barriers (Vitousek et al. 1997; Wilson et al. 2009a). Invasive species can have profound impacts on the systems they invade, either directly, e.g. through predation or competitive exclusion of native species, or indirectly through altering fundamental ecosystem processes, like nutrient cycling, hydrology or fire regimes (Levine et al. 2003). The study of invasions is relevant not only from the perspective of conservation biology, but also provides important insights in the basic determinants of community structure, e.g. mechanisms relating to species coexistence and turn-over, niche theory or plant – soil interactions. The study of invasions has received much attention in the last decades (Richardson & Pysek 2008) and much work in invasion ecology has focused on identifying underlying mechanisms that explain invasion success. However, the basic questions ‘what determines a successful invader’ (species invasiveness) and ‘which communities are susceptible to invasion’ (community invasibility) remain yet largely unresolved and are the topic of ongoing research.

Concepts and definitions

There has been much debate in the scientific literature regarding the terms invasion and invasive species. In his seminal book The ecology of invasions by animals and plants the ‘father of invasion ecology’ Charles S. Elton described invasions as ‘ecological explosions’, meaning ‘the enormous increase in numbers of some kind of living organism’ (Elton 1958). Elton distinguished between ‘outbreaks that occur because a foreign species successfully invades another country, and those that happen in native or long-established populations’. The former he referred to as invaders, the latter he would classify under successional processes. It can be questioned, however, whether this distinction between introduced exotic invaders and native colonizers is valid or whether both are governed by similar processes (Davis et al. 2001; Meiners 2007).

Current definitions of invasions mostly follow Elton’s combination of ‘entering into novel territory’ and ‘uncontrolled spread and abundance’ (Richardson et al. 2000b; Kolar & Lodge 2001; Mitchell et al. 2006; Catford et al. 2009). However, several authors include an element of negative impact into the definition (Mack et al. 2000; Davis & Thompson 2000; Levine et al. 2004). Richardson et al. (2000b)
strongly advocate a focus on novel spread without any connotation of impact. In
their approach to the invasion concept, species progress through several stages:
introduction, naturalization and invasion and are defined accordingly as
alien/exotic, naturalized and invasive plants (Richardson et al. 2000b). To label inva-
sive plants with harmful effects they suggest usage of the term weeds or pests. For
the small percentage of invasive plants that exert a disproportionately large impact
on ecosystems (The ten’s rule (Williamson & Fitter 1996a)), they proposed the name
transformers (Richardson et al. 2000b). This way of defining species invasions is bio-
geographical in its approach and is followed by many authors (Daehler 2003;
Colautti et al. 2004; Richardson & Pysek 2006; Pysek & Richardson 2006; Colautti &
Richardson 2009). However, the implication of this definition is that it excludes
range-shifting native species as invasive. It is therefore criticised by other authors
(Valery et al. 2004; Valery et al. 2008) and the debate is ongoing (Warren 2007;
2009a; Wilson et al. 2009b). In this thesis, due to the lack of a consensus definition,
we follow Richardson et al. (2000b) and define (exotic) invasive plants as those that
form self-sustaining populations that actively spread and become abundant outside
their natural (native) boundaries.

Species invasiveness

In 1965 Baker described the ‘ideal weed’ (Table 1.1). He defined a plant as a weed
when its populations grow entirely or predominantly in areas disturbed by man
(Baker 1965). Currently weeds are defined as plants that grow in areas where they
are not wanted and have harmful environmental or economic effects, especially in
agricultural systems (Richardson et al. 2000b). Weeds are not necessarily exotic
and/or invasive, although of course they can be. In many older publications the term
weed has been used to describe the colonization of new habitats by foreign plants, a
phenomenon that is currently referred to as invasion.

In practice it is unlikely that species can become invasive based on their charac-
teristics alone. There is no set of traits that is consistently associated with invasion
and generalizations across different taxa of vascular plants are difficult to make
(Williamson & Fitter 1996b; Pysek & Richardson 2007), probably because the traits
that make a species successful vary among habitats. Nevertheless, there are some
traits that are more common among invasive than non-invasive plants including
many of Baker’s ideal weed characteristics, such as the ability to reproduce asexually,
high growth rate, short generation time, high phenotypic plasticity and high toler-
ance of environmental heterogeneity (Sakai et al. 2001; Richardson & Pysek 2006).
Also, identifying sets of traits associated with invasiveness has proven successful at
finer taxonomic scales (Rejmanek & Richardson 1996; Grotkopp et al. 2002). For this
reason, Baker’s work is highly relevant for my thesis as he based his research on
several species in the genera *Eupatorium* and *Ageratum*, both of which belong to the tribe of the Eupatorieae in the family Asteraceae and are closely related to the species under study in this thesis: *Chromolaena odorata* (L.) King & Robison (syn. *Eupatorium odoratum*).

Baker’s characterization of an ideal weed was the prelude to many studies on determinants of successful invaders (Rejmanek & Richardson 1996; Williamson & Fitter 1996b; Pysek & Richardson 2007). This has led to a series of main hypotheses (Richardson & Pysek 2006; Alpert 2006; Mitchell et al. 2006; Catford et al. 2009). Plants can become invasive by escaping from natural enemies in their native range (*enemy release hypothesis*) (Keane & Crawley 2002). Plants can adjust their resource allocation by losing traits that are no longer necessary, e.g. reallocating resources from herbivore defense to growth (*evolution of increased competitive ability hypothesis*) (Blossey & Nötzold 1995) or by escaping physiological trade-offs, e.g. trade-offs between r- and K-strategy (Closset-Kopp et al. 2007) or between growth and stress tolerance, leading to rapid growth but increased vulnerability to extreme climatic events (*reckless invader hypothesis*) (Simberloff & Gibbons 2004; Alpert 2006). Furthermore, plants can fill an ‘empty niche’ because they have specific traits that do not occur in the native population (*empty niche hypothesis*) (Elton 1958). Plants may produce allelopathic chemicals against which natives have not evolved defence (*novel weapons hypothesis*) (Callaway & Ridenour 2004) or have the ability to modify their own abiotic environment in favour of their own growth (*ecosystem engineering*) (Crooks 2002). Finally, rapid evolution of invasive plants due to different selective pressures in the novel habitat may explain their invasiveness (*adaptation hypothesis*) (Duncan & Williams 2002; Maron et al. 2004). These hypotheses might explain which species are likely to be successful in a new environment. However, which species actually invade new territories depends not only on the invasiveness of the species, but on the susceptibility of the community as well.

**Table 1.1** Characteristics of the ideal weed (Baker 1965; Baker 1974).

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<table>
<thead>
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<tr>
<td>1.</td>
<td>Germination conditions fulfilled in many environments</td>
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<tr>
<td>2.</td>
<td>Discontinuous germination (internally controlled) and great longevity of seed</td>
</tr>
<tr>
<td>3.</td>
<td>Rapid growth through vegetative (seedling) phase to flowering</td>
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<td>4.</td>
<td>Continuous seed production for as long as growing conditions permit</td>
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<tr>
<td>5.</td>
<td>Self-compatible, but not completely autogamous or apomictic.</td>
</tr>
<tr>
<td>6.</td>
<td>When cross-pollinated, unspecialized visitors or wind utilized</td>
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<tr>
<td>7.</td>
<td>Very high seed output in favorable environmental circumstances</td>
</tr>
<tr>
<td>8.</td>
<td>Produces some seed in wide range of environmental conditions: tolerant and plastic</td>
</tr>
<tr>
<td>9.</td>
<td>Has adaptations for short and long-distance dispersal</td>
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<tr>
<td>10.</td>
<td>If a perennial, has vigorous vegetative reproduction or regeneration from fragments</td>
</tr>
<tr>
<td>11.</td>
<td>If a perennial, has Brittleness, so not easily drawn from the ground</td>
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Community invasibility

Invasibility has been defined as the susceptibility of a community to invasion (Lonsdale 1999; Davis et al. 2005). Communities differ in invasibility because of differences in species richness, community assembly, trait spectra, disturbance regime (history of land-use, herbivory, fire, flooding), successional maturity of the community, resource availability (nutrients, water) and/or climate (temperature, rainfall).

Biotic interactions

Interactions within ecological communities are diverse and complex, and when introduced into a new environment, species lose the complex biotic interactions with their native enemies, mutualists and competitors. Instead they acquire new biotic interactions under new abiotic conditions (Richardson & Pysek 2006; Mitchell et al. 2006). These new biotic interactions can reduce invasibility of the community, for example when native competitors, herbivores and/or pathogens negatively impact invasive plants (biotic resistance hypothesis) (Elton 1958; Levine et al. 2004) or when the new habitat lacks important mutualists of the invasive plants, e.g. pollinators, mycorrhizal fungi or nitrogen-fixing bacteria (missed mutualisms hypothesis) (Richardson et al. 2000a; Mitchell et al. 2006). However, new biotic interactions with invasive species can also increase invasibility of native communities, often through indirect effects (White et al. 2006). For example, exotic invasive plants may accumulate generalist enemies that are less harmful to themselves then to native species (enemy of my enemy or accumulation of local pathogens hypothesis) (Colautti et al. 2004; Eppinga et al. 2006), or they may facilitate other invasive species (e.g. through promoting fire) that cause an invasion domino effect (invasional meltdown hypothesis) (Simberloff & Von Holle 1999).

Disturbance and heterogeneity

Next to these biotic interactions that influence community invasibility, the susceptibility to invasion of communities is also dependent on factors such as disturbance, environmental heterogeneity and resource fluctuations (Catford et al. 2009). Disturbance may increase invasibility by providing invading plants an equal chance of success at colonization and establishment (disturbance hypothesis) (Hobbs & Huenneke 1992). Disturbance may also interact with productivity by enhancing invasion success (dynamic equilibrium hypothesis) (Huston 2004) or by causing fluctuations in resources that can create windows of opportunity for invasion (fluctuating resources hypothesis) (Davis et al. 2000). Other types of windows of opportunity also exist, such as rainfall events (invasion windows hypothesis) (Johnstone 1986). However, disturbance does not always increase invasibility. Fire has promoted invasion in some cases and prevented it in others (D’Antonio & Vitousek 1992). D’Antonio et al. 1999 suggested that recent alterations of natural disturbance regimes by humans could
promote invasion by introduced plants, as native plants are not adapted to this new disturbance regime whereas invasive plants might be (local adaptation hypothesis) (D’Antonio et al. 1999). Finally, high levels of heterogeneity might increase invasibility, as an heterogeneous environment harbours a more diverse array of niches that can potentially host more species (environmental heterogeneity hypothesis) (Melbourne et al. 2007).

**Human-mediated introductions and the role of chance**

Next to these intrinsic factors that determine community invasibility, there are also extrinsic factors or mere chance effects that determine the level of successful invasion into a community, which in turn may affect invasibility. In many intentional introductions the invasive plant has been introduced repeatedly with large numbers of propagules, which increases the probability that it will establish and become dominant (introduction pressure or propagule pressure hypothesis) (Lockwood et al. 2005). Also, the global species pool from which invaders are drawn is far larger than the regional species pool of natives, which has several implications. First, there is a greater chance that introduced species are unrelated to native species, which could promote establishment by reducing competition with close native relatives or decrease the likelihood of attack by pathogens (Darwin’s naturalization hypothesis) (Darwin 1859), although support for this hypothesis has not been unambiguous (Daehler 2001; Duncan & Williams 2002; MacDougall et al. 2009). Secondly, it is more likely that there will be a competitive dominant (e.g. fast grower) among the invaders (global competition hypothesis), similar to the ‘selection effect for a dominant species’ in the biodiversity-ecosystem functioning discussion (Hooper et al. 2005). Alpert (2006) explained the global competition hypothesis as follows: ‘Just as one expects that athletes from the city that hosts an Olympics are unlikely to win many of the medals, one might expect that the native species in a habitat will be unlikely to out-compete all of the species that can be introduced there’. This holds more so because many species have been intentionally or unintentionally selected for traits that enhance invasiveness and transported to suitable climates (habitat filtering hypothesis) (Alpert 2006).

**Objectives of this thesis**

The main objective of this thesis is to increase our understanding of mechanisms that govern the invasion of *Chromolaena odorata* (L.) King & Robison (Asteraceae) in South African savannas. There is no doubt that *C. odorata* is a highly successful invader, but we have no answer to the question of why this species is so successful; specifically its invasion in African savanna habitat, since previously this species was known mainly as an invader of forest margins of tropical rainforest. Increasing our understanding of the ecology of this species and its interactions with the native
community will allow us to develop better methods to control this invasive shrub. In this thesis I explore several of the earlier-mentioned hypotheses that might play a role in this high impact invasion. This thesis is centered on different types of biotic interactions of *C. odorata* with the native community. I specifically focus on plant-plant interactions and plant-soil interactions, under different abiotic conditions and in the presence of natural disturbances of savannas, like trampling and grazing by herbivores and fire.

I studied the invasion of *C. odorata* in a natural savanna reserve in South Africa, Hluhluwe-iMfolozi Park. The advantage of studying this invasion in a natural system is that ecological feedbacks and intricate relationships between different parts of the ecosystem are still in place at the landscape-level, *e.g.* a diverse guild of herbivores, natural disturbances as fire and a highly diverse flora. Hluhluwe-iMfolozi Park is characterised by high habitat heterogeneity on a relatively small scale, and the level of invasion by *C. odorata* differs enormously among habitat types. This is expected to help in finding out which habitat characteristics contribute to invasion success. In this savanna system *C. odorata* forms monospecific dominating stands in certain habitats, grows interspersed with native vegetation in others, while barely persists in again other habitats. I hypothesize that the extent of dominance of *C. odorata* is partly explained by the existence of two alternate states in savanna systems, *i.e.* grasslands and woodlands. Woodlands seem to be far more susceptible to invasion than grasslands, thereby creating source-sink dynamics with continual re-invasion from woodlands into grasslands. However, invasion into grasslands does occur regularly, especially under high-rainfall conditions, but we do not yet know whether it is just a matter of time before *C. odorata* will invade grasslands too (possibly transforming them to thickets or woodland) or whether there are mechanisms preventing large-scale invasion into grasslands.

**Study species**

*Chromolaena odorata*, also known as Triffid weed or Siam weed, is a global high impact invasive species and its invasion is currently not well understood. Because it generally occurs in remote tropical areas, its invasion has been studied much less than invaders of the temperate zone. *Chromolaena odorata* is a perennial, semi-lignified, shrub averaging 1.5 – 2 m in height and reaching up to 6 m as a climber on other plants. The species is native in South and Central America but is rapidly invading a wide variety of ecosystems on other continents, ranging from tropical rainforests to savannas in most of the Paleotropics (McFadyen & Skarratt 1996; Kriticos *et al.* 2005; Raimundo *et al.* 2007). It invades not only human-altered environments, like road verges and abandoned agricultural fields, but also nature reserves, where it forms dense monospecific stands in (broadleaved) woodlands and along river courses and forest margins (Figure 1.1). Thereby, the species denies
human and animal access to invaded areas and out-shades native vegetation (Goodall & Erasmus 1996). In South Africa this species is highly invasive in savannas, where it seems to thrive under different climatic conditions than in its native range (Goodall & Erasmus 1996; Kriticos et al. 2005; Robertson et al. 2008).

Figure 1.1 A. Invaded broadleaved woodland in the Maphumulo area of Hluhluwe-iMfolozi Park. B. Chromolaena odorata forming dense infestations along the Hluhluwe river.
The invasive success of *C. odorata* is thought to depend on the combination of its high reproductive capacity, high relative growth rate and net assimilation rate (Ramakrishnan & Vitousek 1989) and its capacity to suppress native vegetation through light competition (Kushwaha *et al.* 1981; Honu & Dang 2000). The species can reproduce apomictically (Gautier 1992) and has a prolific seed production of light wind dispersed seeds that are easily dispersed by mammals or vehicles as well (Blackmore 1998). A single shrub can produce as many as 800 000 seeds (Witkowski & Wilson 2001). Also the species is a vigorous re-sprouter and able to survive severe disturbances, like fire or cutting, and resist abiotic stress, especially droughts, by quickly re-growing from the basal stems (Devendra *et al.* 1998). Similar to other climbing herbs with very light wood, the species can be viewed as a ‘structural parasite’ that profits from the structural investment in durable stems of other species. The species is quick to lose its leaves and suffers stem die-back when conditions become bad, but can re-grow rapidly from the living stem-base when conditions change. This strategy results in impenetrable shrubs with many dead and dry stems that form a physical barrier as well as a fire hazard in fire-sensitive habitats like gallery and riverine forests (Macdonald 1983; Macdonald & Frame 1988; Goodall & Erasmus 1996).

In its native range *C. odorata* is typically a plant of secondary succession, growing in forest clearings and along the edges of rivers and savannas (Cruttwell McFadyen 1988a). It succeeds the pioneer ephemeral herbs and is subsequently displaced by small trees and bushes and disappears completely when the forest canopy begins to close. Where agriculture and human activity prevent forest regeneration, *C. odorata* persists as a typical plant of forest edges and paths, abandoned fields and pastures, building sites, and along roads, railways and streams (Cruttwell McFadyen 1988a). The species is common and widely distributed from southern Florida to northern Argentina in areas below 1,500 to 1,100 metres altitude and receiving over 1500 mm annual rainfall (Cruttwell McFadyen 1988a; McFadyen & Skarratt 1996; Kriticos *et al.* 2005; Raimundo *et al.* 2007). In the Neotropics, *C. odorata* is confined to the tropical zone and has not spread into the sub-tropical areas, as it has in the Paleotropics, nor does it show the aggressive invasive behaviour that is displayed in the Paleotropics (Cruttwell McFadyen 1991). The main factors controlling *C. odorata* in its native range are presumed to be competition with the numerous other closely related Asteraceous species and attacks by a large complex of insects and pathogens, both specialists and generalists (Cruttwell 1972; Cruttwell McFadyen 1988b; Barreto & Evans 1994). In a study assessing the level of damage to *C. odorata* plants due to insect attack, between 25 and 50% of all growing tips were found to be destroyed (Cruttwell 1972). In contrast, in the Paleotropics only a few phytophagous insects have been recorded to feed on *C. odorata* (Kluge & Caldwell 1992). Many specialist insect herbivores to attack leaves, stems and seeds have been tested for biocontrol programmes (Kluge 1991; Barreto & Evans 1996; Zachariades *et al.* 1999; Muniappan *et al.* 2005).
The impact of *Chromolaena odorata*

The ecological impacts of invaders are often difficult to quantify. There is as yet no objective definition of impact and the magnitude of impact is a commonly disputed issue even among undisputable high-impact invasions (Parker *et al.* 1999). One generally held view is that greatest impacts arise when invaders strongly affect important ecosystems processes, such as nutrient cycling or fire regimes (Vitousek 1990; D’Antonio & Vitousek 1992; Brooks *et al.* 2004). Parker *et al.* 1999 described a much-followed approach to impact, where the impact of an invader is determined by three factors: the geographical range, the abundance and the individual level effect of the invader. Also it is important to assess the impact of an invader relative to the impact of (functionally equivalent) native species. For *C. odorata* its worldwide geographical range is extensive and its abundance is high throughout most of its range, yielding a high score for the first two factors. The latter individual level effect of *C. odorata*, however, is far more difficult to determine and has been the topic of many studies. In table 1.2 I have compiled a list of individual level impacts of *C. odorata* based on the literature.

The individual level impacts of *C. odorata* are highly diverse (table 1.2). It is, however, difficult to accurately assess the impact of this invasive species, as many impacts are based on very few studies, such as the impacts on the native flora. For example, the four references mentioned in table 1.2 were the only references out of almost 300 papers that assessed the effect of *C. odorata* on the native flora. Out of these four papers, only two had the actual aim of studying the impact of *C. odorata* on the local flora (De Rouw 1991; Murali & Setty 2001), the other two only mentioned the effect on the native flora on the side, while its primary focus was on fallow systems (Slaats 1995) or fungal pathogens (Mangla *et al.* 2008). Most literature deals with the socio-economic impact of *C. odorata*, implying that that the invasion of this species is mainly a socio-economic problem (through impairing opportunities for agriculture, livestock husbandry and forestry). I believe that in most of the tropics, this might indeed be the case. In those habitats the invasion depends on forest degradation (in slash-and-burn agriculture, along road and railway tracks, in human settlements) and it has been well-described in the literature that *C. odorata* disappears once the forests are able to regenerate and the canopy closes (De Rouw 1991; Joshi 2006). In savanna systems, however, *C. odorata* is able to invade natural systems and has potentially far greater impacts. This becomes apparent in table 2; the impacts on the fauna and the ecosystem-level impacts are mostly described based on the invasion of *C. odorata* in South and West African savannas.
### Table 1.2 Impacts of *C. odorata*.

#### Impacts on flora
- Reduces local diversity of native vegetation (Murali & Setty 2001; Mangla *et al.* 2008)
- Suppresses native vegetation – grasses and forbs (Slaats 1995)
- Competition - out-shading & physical smothering (De Rouw 1991)
- Destroys the last remnants of lowland forest in South Africa (Macdonald 1983; Liggitt 1983)

#### Impacts on fauna
- Reduces available browse for black rhino (Wagner 2001) en (Howison 2009b)
- Hampers crocodile breeding through outshading (Leslie & Spotila 2001)
- Reduces available food for gorilla by out-competing the main food source (*Zingiberaceae*) (Van der Hoeven & Prins 2009)
- Impoverishes the native spider community (Mgobozi *et al.* 2008)

#### Socio-economic
- Aesthetic (Liggitt 1983)
- By shading out Imperata cylindrica denies local people an important source of thatch (McWilliam 2000)
- Takes over pastures of subsistence farmers, decreasing carrying capacity for life stock and in extreme cases in the Philippines has lead to villages being abandoned (McWilliam 2000)
- Reduces visibility for ecotourism (Cock 1984)
- Reduces quality of pasture (Bani & Le Gall 1996; Bani 2002)
- Reducing yields of plantation crops (Lucas 1989)
- Impedes access (Liggitt 1983; Cock 1984)
- *C. odorata* acts as a nutrient sink in fallow systems (Norgrove *et al.* 2000)
- Toxic to livestock, but never proven, might be due to high nitrate levels in the leaves (Coates 2001)

#### Host for pests
- Acts as alternative food plant to the aphid *Rhopalosipham maidis* which is a major pest of maize (Ganguli & Raychaudhuri 1980)
- Acts as host for the aphids *Aphis citricolas* (Naido 1980), a vector of citrus tristeza virus, and *A. spiraecola* (Hall *et al.* 1972)
- Transmits the seed borne fungi: *Fusarium solani* and *F. semitectum* (Esuruoso 1971)
- Provides breeding grounds for the grasshopper *Zonocerus variagatus*, which is a major pest on crops in West Africa (Moder 1984; Boppre *et al.* 1992; Boppre & Fischer 1994; Moder 1996)

#### Ecosystem level effects
- Allelopathic (Ambika & Jayachandra 1980; Sahid & Sugau 1993; Gill *et al.* 1996; Ambika 2002a; Sangakkara *et al.* 2008)
- Accumulates local soil-borne fungi (*Fusarium* spp.) that hamper performance of native species (Mangla *et al.* 2008)
- Halts natural succession by creating dense thickets (De Foresta & Schwartz 1991)
- Increases fire hazard due to flammable foliage (Liggitt 1983; Muniappan & Viraktamath 1993; Bamba *et al.* 1993; Tonzibo *et al.* 2007)
- Carries savanna fires into fire-sensitive forests (Macdonald 1983)
- Impacts the forests-savanna mosaic (Gautier 1996)
- Increases its biomass after fire (Norgrove *et al.* 2000)
Study area – Hluhluwe-iMfolozi Park

Hluhluwe-iMfolozi Park is a 90,000 ha reserve in Kwazulu-Natal (KZN), South Africa, situated between latitudes 28°00’ and 28°26’ S and longitudes 31°43’ and 32°09’ E (Figure 1.2). Initially two separate reserves, Hluhluwe and iMfolozi (former spelling Umfolozi) were officially proclaimed by the British in 1895 and are the oldest reserves in colonial Africa (Brooks 2005). Not until 1989 were the reserves connected by the formal proclamation of the disputed corridor of tribal land between them, from where people were forcibly removed during the 1940s (Brooks 2005).

The reserve has a coastally modified climate with much of the variability in local weather being related to topography (Conway et al. 2001). Annual rainfall is strongly seasonal with most rain falling in the spring and summer, between October and March. The mean annual rainfall ranges from 1000 mm in the high altitude regions in the north to 600 mm in the low-altitude south-western areas. Daily maximum temperatures range from 13º to 35ºC. The reserve is of strong conservation importance because it hosts a rich and complete set of indigenous large herbivores and carnivores, including black and white Rhino, buffalo, elephant, nyala, lion, leopard and wild dog (Brooks & Macdonald 1983). The reserve falls within the southern African savanna biome and is characterized by vegetation types ranging from open grasslands to closed Acacia and broad-leaved woodlands (Whateley & Porter 1983). Next to the savanna habitat, fire-sensitive gallery forests occur in high altitude areas and riverine forests and wetland communities occur along rivers. Plant species diversity is high with over 1250 vascular plant species recorded, comprising almost 400 woody trees and shrubs and about 150 grass species (Conway et al. 2001).

The vegetation of Hluhluwe-iMfolozi Park, apart from the Corridor area, has never been subjected to extensive human disturbances and vegetation dynamics are primarily driven by rainfall, fire and herbivory. An important management practice in the reserve is the controlled use of fire to burn grassland and control woody shrub encroachment. In general fire is confined to the grassland and open woodland communities, with closed woodland and forests tending to exclude fire. Controlled burning is generally carried out at the end of the dry season (July to September) and on average 26% of the surface area of the reserve is burned each year (Balfour & Howison 2001). The vegetation of Hluhluwe-iMfolozi Park is prone to exotic plant invasions, particularly in the more mesic areas. During the latest exotic plant survey (Henderson, April 2004) sixty-three invasive and potentially invasive exotic plants were recorded. The most serious of these include Caesalpinia decapetala, Chromolaena odorata, Ipomoea carnea subsp. fistulosa, Lantana camara, Montanoa hibiscifolia, Melia azedarach, Parthenium hysterophorus, Senna bicapsularis, Senna didymobotrya, Solanum mauritianum, Solanum seaforthianum, Psidium guajava, and Tithonia diversifolia (Macdonald 1983; Macdonald & Frame 1988; Henderson 1989; Henderson 2001).
Figure 1.2 (A) The location of Hluhluwe-iMfolozi Park within South Africa, the five management sections of the Park; Manzibomvu and Nqumeni forming Hluhluwe in the north; Masinda, Mbhuzane and Makhamisa forming iMfolozi in the south. Dots depict C. odorata high density sample plots. (B) Major rivers and mean annual rainfall of Hluhluwe-iMfolozi Park. (C) Elevation of Hluhluwe-iMfolozi Park, ranging from 560 m in the north to 40 m in the south east. (Figure reprinted from: R.A. Howison, 2009).
The invasion of *Chromolaena odorata* in Hluhluwe-iMfolozi Park

The invasion of *Chromolaena odorata* in Hluhluwe-iMfolozi Park has been well documented. The species was first observed in 1961 (Macdonald 1983), approximately 15 years after its introduction into South Africa. It was presumably brought in accidentally during World War II in seed-contaminated packaging material offloaded at Durban harbour, 350 km south of Hluhluwe-iMfolozi Park (Liggitt 1983). Although other authors suggest that *C. odorata* has been introduced to South Africa already in the mid-nineteenth century, when it was found to grow in the Cape Town Botanic Garden (Zachariades et al. 2004). *Chromolaena odorata* spread rapidly through the more mesic habitats of the reserve, mainly in Hluhluwe, the northern part of the reserve (Figures 1.3 and 1.4) and in 2001 more than 20% of Hluhluwe was covered with dense infestations (Howison 2009a). Levels of invasion differ per habitat type and are higher in woodlands than in grasslands (Figure 1.5).

![Figure 1.3 Year of first occurrence of *C. odorata* per grid cell (0.25 km²), representing the expansion of *C. odorata* (1978 – 2001) (Data sources: north: O.E. Howison, 2009; south: EKZNW unpublished data). The map indicates that spatially some areas of the park have been heavily invaded in the north while the southern areas have remained relatively free of invasion. (Figure re-printed from: R.A. Howison, 2009).](image-url)
Invaded areas are currently under large-scale active mechanical and chemical control. Current clearing practice consists of hand-pulling and spraying of seedlings and slashing of established plants followed by herbicide application to the remaining stumps (Erasmus 1988; Van Gils et al. 2004). Clearing is funded through the Working for Water Program, which is a national effort responsible for managing exotic invasive plants in South Africa (Van Wilgen et al. 1998) and the Chromolaena Clearing Project ‘Impi ka Sandanezwe’. The latter program was established in 2004 by Ezemvelo KZN Wildlife, the provincial nature conservation authority, and the KZN provincial government and focuses on the clearing of C. odorata in Hluhluwe-iMfolozi Park and adjacent areas. However, incurred costs of these programs are high (Marais et al. 2004; Turpie et al. 2008) and continued follow-up efforts are necessary (Van Gils et al. 2004). This limits success in permanently excluding C. odorata and the species continues to spread in natural savannas, communal areas and plantations.

**Figure 1.4** Cumulative distribution of *Chromolaena odorata* (1978 – 2001) in Hluhluwe, the northern part of Hluhluwe-iMfolozi Park. (Data: O.E. Howison 2009, Figure re-printed from: R.A. Howison 2009).

**Figure 1.5** Percentage of the two main habitats in Hluhluwe, the northern part of Hluhluwe-iMfolozi Park, that were invaded by *Chromolaena odorata* in 2001 (Data: O.E. Howison 2009).
along the east coast of Southern Africa (Goodall & Erasmus 1996; Van Gils et al. 2004). *Chromolaena odorata* has invaded most of West Africa and is currently expanding from the South and West African populations towards East Africa, though the exact extent of its African distribution remains unknown.

Biocontrol has been attempted in Hluhluwe-iMfolozi Park. However, establishment of the leaf-mining moth *Pareuchaetes insulata*, which has proven a successful agent against *C. odorata* invasions in Ghana and Indonesia (Zachariades et al. 1999), has been unsuccessful in South Africa until now. This is possibly due to biotype incompatibility, cold temperatures or to the presence of a distinct dry season; as *C. odorata* sheds all its leaves when conditions become too stressful, the moths do not survive due to lack of food (Strathie & Zachariades 2004). To date, no specialist insects have been found that are able to survive the potentially damaging cold temperatures, fires or dry seasons that are typical of Southern African savannas and with the help of climate matching exercises the search for suitable biological control agents continues (Robertson et al. 2008).

**Thesis outline**

In this thesis I will explore several possible mechanisms that may explain invasive success of *C. odorata*. As invasions are always an interplay of both the invasiveness of the plant and the invasibility of the native community, I will approach this question both from a species perspective, e.g. species intrinsic traits, escape from trade-offs or natural enemies, and from a community perspective, e.g. the role of disturbance and competition in resisting invasion, the presence of positive or negative community feedbacks and the role of multiple stable equilibria.

The South African ecotype of *C. odorata*, which is thought to have a northern Carribean origin (Von Senger et al. 2002; Zachariades et al. 2004) is believed to have different climatic requirements than other invading populations in West Africa, Asia, Australia and the Pacific (Kriticos et al. 2005; Robertson et al. 2008) as the species invades in this region under much drier conditions than prevalent in its native American range. Therefore, competition for water, especially between *C. odorata* and native grasses, might be an important factor determining invasion success and is a central theme in my thesis. Chapters 2 and 4 each deal with this theme in a different way. In chapter 2 I will explore the effect of competition under different water availabilities in controlled conditions in the greenhouse and focus on the seedling stage and the comparison with native range *C. odorata*. I will discuss results in the framework of current niche theory and explore whether the observed climatic shift is due to genetic changes (fundamental niche shift) or changes in competitive interactions (realized niche shift). In chapter 4 I will examine the effects of competition with native grasses under different water availabilities in the field, focusing on both the seedling and adult stages in combination with disturbance.
Disturbances, such as fire or soil disturbances, are thought to temporarily ‘reset’ the system, thereby reducing competition and creating windows of opportunity that may allow species to invade.

In addition to plant-plant interactions, I studied the effect of plant-soil interactions on the invasive success of *C. odorata*. Release from native soil pathogens may contribute to the successful colonization of non-native species. In chapter 3 I seek an explanation for success of *C. odorata* in the absence of natural enemies in its non-native range. I investigate if dynamic plant-soil feedback interactions affect growth and biomass allocation of *C. odorata*.

In chapter 5 I use the mechanistic understanding gained in the previous chapters to explore effective control strategies for *C. odorata*. I combine conventional clearing methods with fire in a large-scale field experiment. I show that the presence of (dry) *C. odorata* can create intense canopy fires that are able to switch the system from invaded woodlands into grasslands that have a far lower susceptibility to re-invasion. Therefore, fire-induced vegetation shifts could be used to control the invasion of *C. odorata* in the fire-prone habitats of South African savannas.