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Evaluating the efficacy of invasive plant control in response to ecological factors

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ABSTRACT

Biological invasions have increased dramatically in the past centuries and are one of the greatest threats to biodiversity today. *Chromolaena odorata*, a herbaceous shrub from the Americas, is one of the most widespread and problematic invasive plant species in the tropics and sub-tropics. The plant is a serious problem in South Africa, where invasive species threaten biodiversity and use up water resources. This study combines data on the distribution of *C. odorata* with ecological and clearing management data to evaluate the efficacy of an invasive plant clearing program over its decade of operation in the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa. Densities and local extent of the *C. odorata* invasion were significantly reduced during the period of operations of the clearing program. Seasonal effects impacted clearing efficacy, namely a reduction in efficacy during the seed dispersal period. Clearing success was positively associated with clearing effort and fire frequency and negatively associated with rainfall. Management implications drawn from the results include halting clearing during the seed-drop period, giving extra attention to areas with more rainfall and other water availability, and incorporating fire with other clearing methods where possible.

1. Introduction

Over the past few centuries, biological invasions have become increasingly more prevalent. Using humans as a dispersal agent through transport and commerce, a rising number of species have traversed natural bio-geographical barriers and spread to areas outside of their native ranges (D'Antonio and Vitousek, 1992; Vitousek et al., 1997; Mack et al., 2000). Invasive species comprise of a small fraction of all alien species introduced outside of their native ranges that "proliferate, spread, and persist to the detriment of the environment" (Mack et al., 2000; Richardson et al., 2000). Invasive species can disrupt disturbance regimes, ecosystem productivity, nutrient cycles, hydrology, community structure (Vitousek et al., 1997; Levine et al., 2003; Gaertner et al., 2014), and are considered the greatest threat to biodiversity worldwide after land-use change (Millennium Ecosystem Assessment, 2005). In addition to the detrimental effects that invasive species have on the flora and fauna of the systems they invade, their impact can have deleterious consequences to human health and well-being (Vitousek et al., 1997). The invasion of ecosystems can severely threaten the availability of ecosystem services and can diminish the production of agricultural goods, silviculture, and natural goods (Mack et al., 2000; Van Wilgen et al., 2008).

South Africa spends a considerable amount of resources combating invasive species (Van Wilgen et al., 2008). Having an economy relying heavily on farming, ecotourism, and timber production makes the control of invasive species critical for the country. More importantly, South Africa is a water-stressed nation, and many regard water scarcity as the biggest limitation to development in South Africa today (Turpie et al., 2008). A large number of alien plant species in South Africa consume more water than native vegetation, and as a result, there is an estimated reduction of 7% of the country's total water runoff being wasted by current invasions (Gorgens and Van Wilgen, 2004; Van Wilgen et al., 2008). Shockingly, reductions could advance to eight times that amount if invasive species were to cover their entire potential range in South Africa. The sobering threat of invasive species to the nation's water supply prompted the government to establish the Working for Water (WfW) program in 1995. This flagship program focuses on removing alien invasive plants to increase water resources and serve conservation efforts, while simultaneously alleviating poverty by employing individuals from underprivileged local communities on the clearing teams (Van Wilgen et al., 1998). The WfW program invests heavily in research

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and has developed norms and standards for invasive alien plant clearing that are available to be used by other programs.

One of South Africa's many problematic invasive species, and a major target of the Working for Water program, is *Chromolaena odorata* (L.) King & Robinson, a perennial, herbaceous shrub of the family Asteraceae, known among many names as Siam weed or Triffid weed. It originates from the Americas, with a native range spanning from the south-eastern U.S. to northern Argentina, including the Caribbean islands. *Chromolaena odorata* grows to a height of 1.5–2 m, but can reach heights up to 10 m when acting as a creeper, using other vegetation for support (Zachariades and Goodall, 2002). In South Africa, *Chromolaena odorata* is a category 1(b) invasive species under the National Environmental Management: Biodiversity Act 2004 (NEMBA), which came into force as of 1 October 2014, and prior to that was classed a category 1 noxious weed under the Conservation of Agricultural Resources Act 43 (1983). These declarations carry the legal requirement for immediate removal from both private and public lands (Van Gils et al., 2004), although in many cases, this is difficult to enforce.

The main objective of South Africa's Working for Water program is to reduce the density of invasive species in South Africa by 22% per annum (Department of Environmental Affairs, 2015). The program spent 171.8 million ZAR (24.5 million USD) fighting *C. odorata* alone from the program's founding in 1995 to 2008 (Van Wilgen et al., 2012). Despite this effort, of all the country's invasive plant species, *C. odorata* moved from ranking 14th in 2000 to 4th in 2010 in terms of occupied area (Van Wilgen et al., 2012), highlighting the difficulties involved in controlling this species.

Since 2004, a large-scale control program focused on clearing *Chromolaena odorata* has been operational in Hluhluwe-iMfolozi Park (HiP), KwaZulu-Natal, South Africa. This program was modeled after the WfW programme and followed their standard procedures. Over the decade of operations of the program, it has hired a large workforce of laborers from communities surrounding the park and successfully brought the species down to maintenance level (<5% park-wide cover), albeit at a cost of 103 million ZAR (15 million USD) (te Beest et al., 2017). However, as the species is still present in the park, continued monitoring is fundamental to prevent re-invasion and maximize the successes of past clearing efforts. Therefore, this study seeks to assess current densities of the species, to compare them to past densities, and to analyze the extent to which ecological factors and management practices may have aided the control program of *Chromolaena odorata* in HiP. This information might benefit future clearing programs for this species elsewhere, as the limited resources available for invasive alien plant control require research into factors improving efficacy and prioritization of areas that facilitate success (Van Wilgen et al., 2016). The current study evaluates management decisions, such as time between clearing treatments, amount of effort exerted, clearing methods utilized, and time of year clearing takes place, as well as ecological factors, such as rainfall, fire regime, temperature, and topography. Data sources include invasion density estimates obtained from transect sampling, clearing data from the park's alien plant control program, and ecological data from park records and climate databases.

2. Methods

2.1. Study area

Hluhluwe-iMfolozi Park (HiP) is a 90,000 ha reserve in the KwaZulu-Natal province of South Africa. It is situated between 28°00′–28°26′ S and 31°09′–32°43′ E. Elevation in the park varies from 60 to approximately 600 m above sea level and experiences a strong rainfall gradient with around 1000 mm annually in the higher altitudes in the north of the park, to 600 mm annually in the lower altitudes in the south of the park (Balfour and Howison, 2001). Rainfall is seasonal with most rain falling in the spring and summer months of October through March. Mean maximum temperature ranges from 23 °C in July to 29 °C in January and mean minimum temperature ranges from 13 °C to 19 °C. Habitat types range from open grasslands and woodlands that are frequently burned to closed acacia, broad-leafed woodlands and forests that are generally fire excluding (Whateley and Porter, 1983). Approximately one-quarter of the park area is burned annually (Balfour and Howison, 2001). HiP has a heterogeneous landscape and a high diversity of flora and fauna. There have been over 1250 recorded vascular plant species, and the park is home to many species of high conservation value, including the white rhinoceros *Ceratotherium simum* (Burchell, 1817), black rhinoceros *Diceros bicornis* (Linnaeus, 1758), and the African wild dog *Lycaon pictus* (Temminck, 1820) (see Macdonald, 1983). HiP is enclosed with a game-proof fence and is surrounded by rural communities and communal agricultural lands (Whateley and Porter, 1983).

2.2. Study species

Chromolaena odorata was first recorded as naturalized in South Africa near Durban in 1947 and has become widespread and abundant in the subtropical eastern and north-eastern parts of the country (Paterson and Zachariades, 2013). The first documentation of *C. odorata* in HiP was in 1961 (Macdonald, 1983). The species spread rapidly through the more mesic northern region of the park and in 2001 more than 20% of the area of the northern sections (Hluhluwe) was covered with dense monospecific infestations (Howison, 2009). In the remainder of HiP *C. odorata* is more restricted to riverine habitats and was shown to occur at the lower limits of its tolerance to water stress (te Beest et al., 2013). *Chromolaena odorata* commonly invades everything from roadsides, communal lands, pastures, croplands, and plantations to riverine areas, grasslands, savannas, forest edges, and disturbed forests (Zachariades et al., 2011). Southern African populations represent a distinct biotype that tolerates cooler temperatures than most biotypes found elsewhere, including in the native range, but the invasion is nonetheless restricted to frost-free areas (Kriticos et al., 2005; Paterson and Zachariades, 2013; te Beest et al., 2013). The plant can produce up to 260,000 wind-dispersed seeds per m^2 per year and has very few natural enemies outside of its native range (Witkowski and Wilson, 2001; Qin et al., 2013). It forms thick, monospecific stands that can shade out native vegetation and create restrictive barriers to animal and human passage (Goodall and Erasmus, 1996; te Beest et al., 2015a). *Chromolaena odorata* preferably grows in woodlands and on forest edges, where it can act as a fire ladder, turning surface fires into high-intensity canopy fires in habitats that would normally exclude fire (Macdonald, 1983; Macdonald and Frame, 1988; te Beest et al., 2012). The species can sprout quickly after fire and thereby outcompete native vegetation (te Beest et al., 2012, 2015b). Biocontrol of *C. odorata* has been investigated for many years, but has yet to be implemented in an effective manner in South Africa (Goodall and Erasmus, 1996; Zachariades et al., 2011).

2.3. Control program

In 2003/4, a large-scale control program funded by Ezemvelo KZN Wildlife (EKZNW), the provincial nature conservation authority, and the KwaZulu-Natal Department of Agriculture, Environmental Affairs and Rural Development (DAEA&RD) was initiated to target the *C. odorata* invasion in HiP. The program had strong links to the Working for Water program and adopted their standardized methodology. In recent years, the Invasive Alien Species Programme (IASP) has been expanded to include other alien species. The IASP contracted out clearing duties of different areas to teams of around 9–10 people. Being a community poverty-relief program, people were hired from local communities surrounding the park. At the height of operations, nearly 1000 laborers were clearing in the park at a time. Prior to forming a contract, the IASP would estimate the density of an area to determine

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how many person-days would be required to clear the area. Contract areas were revisited periodically to determine when follow-up treatments were necessary.

The main clearing practice utilized to control *C. odorata* is known as cut-stump treatment, i.e. slashing followed immediately with a treatment of herbicide to the remaining stump (Euston-Brown et al., 2007). Small plants are generally hand-pulled (Van Gils et al., 2004; Euston-Brown et al., 2007). Due to the rapid regenerative properties of the plant, cut-stump treatment always needs to be followed-up several times. Fire in combination with cut-stump treatment has been shown to increase clearing efficacy (te Beest et al., 2012). However, since adult plants can survive most fires, they always need to be preceded or followed-up by cut-stump treatment (te Beest et al., 2012).

2.4. Density and extent of invasion along transects

The distribution and densities of *C. odorata* in HiP were recorded in 2004, 2010, and 2014 along a network of 24 line transects that range in lengths of 3.9 to 10.4 km (avg. 7.9 km; Fig. 1). These transects are cut biennially (on even-numbered years) as part of a game census of the park. In 2014, the *C. odorata* sampling was extended to include 10 additional un-cut transects that are situated in a wilderness section in the south and were navigated by GPS (lengths 6 to 13 km, avg. 9.1; Fig. 1). Transects are numbered from north to south and are evenly distributed over the reserve, covering all vegetation types and topography (see Cromsigt et al., 2009, for details). Densities of *C. odorata* were recorded in 6 classes (according to a modified Braun-Blanquet scale); 0: no plants visible, 1: few individuals present (1–5% cover), 2: 6–25% cover, 3: 26–50% cover, 4: 51–75% cover, and 5: 76–100% cover (Braun-Blanquet, 1932). Density class 5 represents a dense monoculture where no distinction between individual shrubs could be made anymore. Densities of *C. odorata* were estimated separately on the left- and right-hand side of the transect up to a distance of 5 m perpendicular to the transect. In 2004, *C. odorata* densities were estimated for every 50 m along the transects. In 2010 and 2014, densities were estimated for every 5 m along the transects. To make values for different years comparable, the 2010 and 2014 density scores were averaged for every 50 m and the decimals were rounded to the superior density class

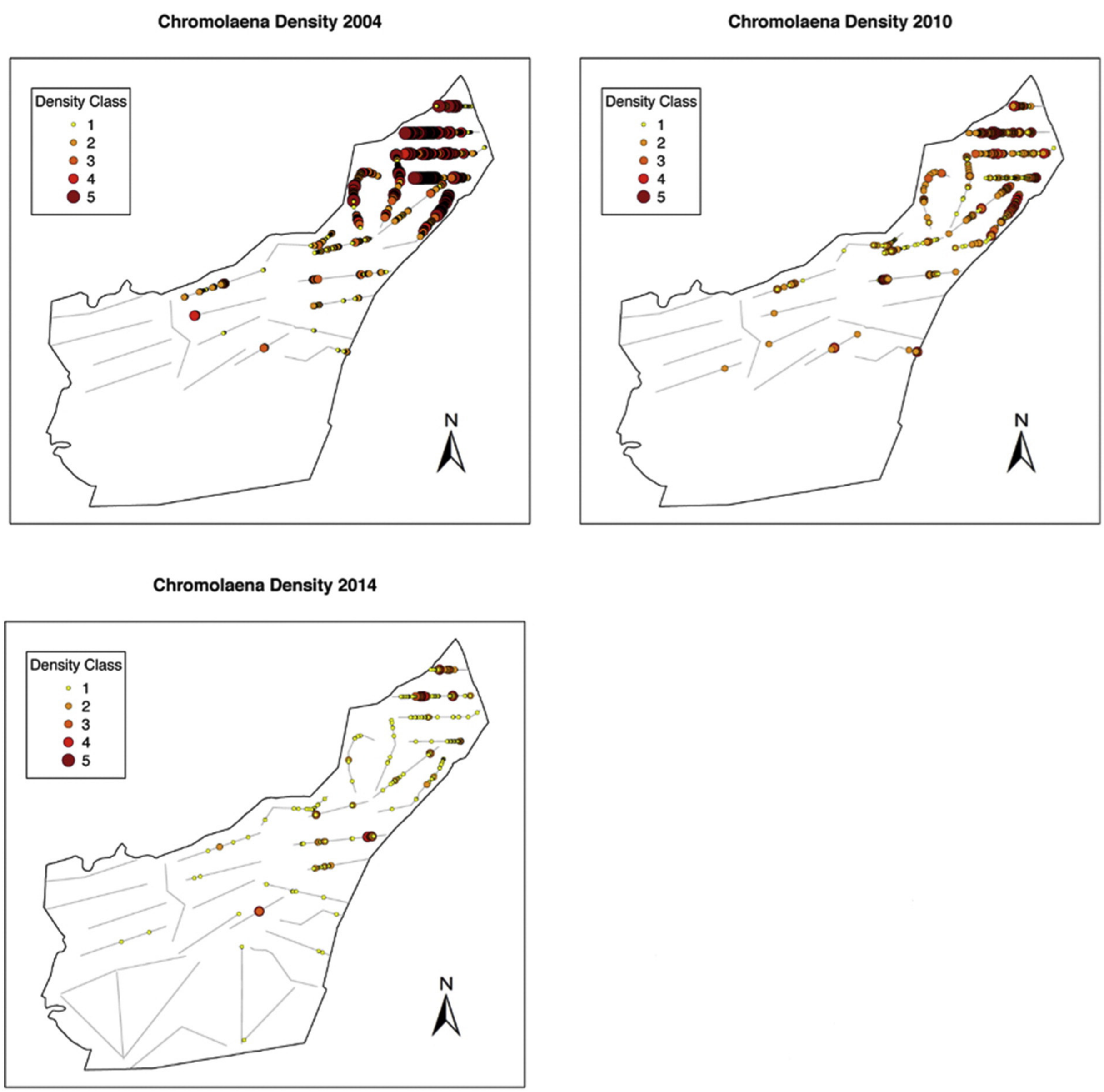

Fig. 1. Density class of *Chromolaena odorata* per 5 m segment of transect for years 2004, 2010, and 2014. Density classes 1–5 are represented as follows: 0: no plants visible, 1: few individuals present (1–5% cover), 2: 6–25% cover, 3: 26–50% cover, 4: 51–75% cover, and 5: 76–100% cover.

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value. For each plot section (50 m × 10 m area), each year, the maximum of the left and right side values were used in the statistical analyses.

Density classes were averaged per transect, and the percentage of transect invaded was calculated to determine the spatial extent of invasion. Differences in the mean transect densities and extent of invasion between 2004, 2010, and 2014 were tested with a one-way ANOVA model. Only the data from the 24 cut transects that were sampled during all three years was used for this analysis. Differences between years were tested with a Tukey HSD comparison.

2.5. IASP clearing data

Data on *C. odorata* clearing practices in HiP was obtained from the Invasive Alien Species Programme for the entire period of operations from 2004 to 2014. This data included the spatial location of contract areas (polygons with a unique ID), the estimated density of each contract area before each clearing treatment, the issue dates of clearing contracts, clearing stage (i.e. Initial clearing, 1st follow-up, etc.), the age of plants (seedlings, etc.), the clearing method employed (cut-stump, hand-pulling, etc), and the amount of contracted person-days.

For each contract area the following was calculated: 1) the number of treatments conducted from 2004 to 2014, 2) the mean number of days between clearing treatments, and 3) the total number of person-days per hectare contracted out over the 10 year period of operations. The latter calculation provided a quantified estimate of the total amount of effort issued to each clearing area from 2004 to 2014 (hereafter referred to as total effort). To quantify the decrease in *C. odorata* density (clearing efficacy) for each contract area after each clearing treatment, the density before each treatment was divided by the density observed just prior to the following treatment: ln ($density_t \div density_{t+1}$). The values were divided to ensure that the proportional density change was represented, instead of the absolute change, and the natural log was used to account for any increases in plant density after treatment.

2.6. Effects of clearing methodologies and ecological factors

Ecological data (fire, rainfall, temperature, and topography) was obtained from park records and online databases. Several environmental factors that have been observed to have an effect on *C. odorata* abundance were chosen for analysis, which included fire frequency from 2004 to 2014, average rainfall, elevation, slope, average minimum temperature in July, and average maximum temperature in January (Kriticos et al., 2005; McLennon, 2006-MSc thesis; Raimundo et al., 2007; te Beest et al., 2012). Annual fire maps were obtained from the HiP research office. Rainfall and average minimum and maximum temperature data were extracted from the WorldClim database at a resolution of 30 arc sec (version 1.4; Hijmans et al., 2005). Topographical data was obtained from NASA's Shuttle Radar Topography Mission (SRTM) imagery at a resolution of 3 arc sec. Distribution data, IASP clearing data, and fire frequency data were overlaid using ArcGIS (version 10.2.1). Rainfall, temperature, and topographical data were extracted to every 5 m point of the distribution data using the {raster} package of R. Distribution data, IASP clearing data, ecological, and topographical data were integrated at the scale of the IASP data, i.e. per contract area ($n = 217$), by averaging the multiple data points for the distribution, ecological, and topographical data per contract area to avoid pseudoreplication.

A principal component analysis (PCA) was then conducted to explore the relationship between *C. odorata* density and clearing methodologies (mean number of days between treatments, total effort per contract area), ecological factors (fire frequency, average rainfall, average maximum January temperature, average minimum July temperature), and topographical factors (elevation, slope). Normal probability ellipses were used to group data points according to the change in *C. odorata* density along the transects from 2004 to 2014.

The strength of the relationships observed in the PCA analysis was tested using a generalized linear model (GLM) with quasi-binomial error. The same predictor variables were used as the PCA. The response variable was the change in density class of *C. odorata* from 2004 to 2014. As this data was zero-inflated, the data was transformed into a binary set of successful and unsuccessful clearings. All contract areas with a lower density of *C. odorata* in 2014 than in 2004 were considered successful and given a value of 1. All contract areas with a higher or equal density of *C. odorata* in 2014 than in 2004 were considered unsuccessful and given a value of 0. Using model selection, insignificant variables were removed from the model until the simplest model with the most explanatory power was formed. Since the data was over-dispersed, the model was run with a quasi-binomial error. To account for any underlying differences in clearing efficacy among the clearing contract areas, the model was run once more using clearing contract areas as a random effect.

2.7. Seasonal effects on clearing efficacy

Any potential seasonal effects on clearing efficacy were tested using the IASP data. The change in *C. odorata* density after each clearing treatment (as explained above) was grouped according to the calendar month in which the treatment was carried out. A mixed-effects model was performed with the change in density as the response variable, calendar month as a fixed effect, and contract area and year as random effects. This analysis was only performed for the cut-stump treatment method, which was used in >85% of all treatments, and the handpulling method. The foliar application treatment occurred at too low frequency to be analyzed. Significant differences between months were tested for with a Tukey HSD comparison.

3. Results

3.1. Density and extent of invasion along transects

Chromolaena odorata densities have been significantly reduced over the period 2004 to 2014 ($F_{2,69} = 6.8$, $p = 0.002$; Fig. 1). The monospecific stands (class 5) have been completely eliminated in 2014 and there were only 16 observations of class 4 (51–75% cover), which is equivalent to 80 m of transect. The highest density patches remain in the northern-most area of the park. Also, the overall extent of the *C. odorata* distribution in HiP has retreated. In 2004 on average 22.3% of 50 m sections were invaded. In 2010 and 2014 this was reduced to 14.7% and 7.8%, respectively ($F_{2,69} = 3.3$, $p = 0.04$, Table 1). (See Table 2 for density class averages).

3.2. IASP clearing data

The number of treatments carried out per contract area was between 1 and 12 treatments over the 10 year period (mean = 7, median = 7; Fig. 2A). The average number of days between clearing treatments of each contract area was between ~150 and ~1800 days (~5 months to ~5 years; mean = 509 days, median = 509 days; Fig. 2B). The effort (sum of person-days per hectare) ranged between 0.5 and 88 days per hectare (mean = 12 days/ha, median = 6 days/ha; Fig. 2C). Average clearing efficacy, determined by the reduction of *C. odorata* density from one clearing treatment to the next, was positive for 87% of contract areas.

3.3. Effects of clearing methodologies and ecological factors

The first three components of the PCA analysis explained 45.1, 22.5, and 12.5% of variance of the data. Clearing effort was most strongly associated with larger reductions of *C. odorata* infestations when plotting component 1 against component 2 (Fig. 3A). Fire frequency was most

Table 1
Proportion of invaded 50 m sections by transect for years 2004, 2010, and 2014.

Transect	N sections	2004	2010	2014
1	78	0.58	0.37	0.40
2	163	0.65	0.52	0.34
3	166	0.71	0.36	0.13
4	107	0.73	0.65	0.18
5	166	0.45	0.13	0.04
6	169	0.53	0.14	0.05
7	172	0.17	0.20	0.10
8	191	0.46	0.41	0.10
9	164	0.13	0.15	0.07
10	123	0.41	0.27	0.06
11	184	0.14	0.15	0.15
12	122	0.11	0.00	0.14
13	175	0.16	0.07	0.03
14	153	0.03	0.01	0.01
15	137	0.01	0.01	0.00
16	173	0.01	0.00	0.03
17	127	0.02	0.04	0.01
18	138	0.06	0.04	0.01
21	187	0.00	0.00	0.00
22	208	0.00	0.00	0.00
23	191	0.00	0.00	0.00
24	165	0.00	0.00	0.00
25	182	0.00	0.01	0.01
26	152	0.00	0.00	0.01

strongly associated with *C. odorata* reductions when plotting component 1 against component 3 (Fig. 3B).

In the GLM, the average number of days between clearing treatments, elevation, slope, minimum July temperature, and maximum January temperature were not significantly associated with changes in *C. odorata* density, and were discarded during model selection. Effort, measured in the number of person days contracted, was positively associated with clearing success ($t = 5.8$, $p < 0.001$, Fig. 4A). Fire frequency was also positively associated with successful clearing ($t = 3.2$, $p = 0.002$), while rainfall resulted in a negative association ($t = -3.3$, $p = 0.002$; Fig. 4B).

Table 2
Average density class of *Chromolaena odorata* by transect for years 2004, 2010, and 2014. Density classes 1–5 are represented as follows: 0: no plants visible, 1: few individuals present (1–5% cover), 2: 6–25% cover, 3: 26–50% cover, 4: 51–75% cover, and 5: 76–100% cover (see Fig. 1).

Transect	Length (km)	2004	2010	2014
1	3.9	1.25	0.54	0.45
2	8.2	2.17	0.99	0.44
3	8.3	1.99	0.38	0.13
4	5.4	2.77	0.80	0.18
5	8.3	1.20	0.13	0.04
6	8.5	1.41	0.15	0.05
7	8.6	0.31	0.22	0.10
8	9.6	1.59	0.60	0.10
9	8.2	0.19	0.16	0.07
10	6.2	0.60	0.29	0.07
11	9.2	0.27	0.25	0.20
12	6.1	0.16	0.00	0.14
13	8.8	0.30	0.07	0.03
14	7.7	0.06	0.01	0.01
15	6.9	0.01	0.01	0.00
16	8.7	0.01	0.00	0.03
17	6.4	0.05	0.04	0.01
18	6.9	0.07	0.04	0.01
21	9.4	0.00	0.00	0.00
22	10.4	0.00	0.00	0.00
23	9.6	0.00	0.00	0.00
24	8.3	0.00	0.00	0.00
25	9.1	0.00	0.01	0.01
26	7.6	0.00	0.00	0.01

3.4. Seasonal effects on clearing efficacy

Cut-stump treatment was the main method utilized by the IASP to control *C. odorata* (>85% of treatments), with each calendar month containing between 105 and 882 treatments carried out during 2004 to 2014. Clearing efficacy, in terms of density reduction, of this method exhibits a clear seasonal trend (Fig. 5A). The months of May, August, September, and December had significantly lower clearing efficacies than the other months of the year ($F_{11,869} = 13.7$, $p < 0.001$).

Hand-pulling was much less utilized, but also showed clear seasonal trends ($F_{8,187} = 19.9$, $p < 0.001$, Fig. 5B). Most treatments were performed during July, which had a mean positive effect, i.e. a reduction in *C. odorata* densities. In contrast, handpulling in the seed-drop months August and September both resulted in mean negative effects. Similar to the cut-stump method, efficacy for handpulling rose again dramatically in October.

4. Discussion

The large scale clearing operation performed by the Invasive Alien Species Programme in HiP successfully reduced *C. odorata* densities to maintenance levels (<5% park-wide cover) between 2004 and 2014. Also the extent of the invasion has been significantly reduced, although *C. odorata* individuals are still found throughout most of its former distribution (Fig. 1). The most significant factor attributed to the clearing successes is the amount of effort exerted in the clearing program, which involved a tremendous amount of manpower. Rainfall and fire frequency are the two most important ecological factors influencing the clearing efficacy of *C. odorata*. Rainfall is negatively associated with clearing success, indicating that areas with higher rainfall have a lower clearing efficacy than areas with less rainfall. Fire frequency exhibits a positive relationship to clearing success, indicating that areas that burned more often experienced higher clearing efficacy. Seasonal influences were found to have a strong impact on clearing efficacy and highlight periods where efforts should be either increased or scaled-back to maximize the success of clearing programs and use resources in the most efficient manner.

The most paramount change over the decade of clearing included in this study is the complete extermination of high impact densities (75–100% cover). The absence of the highest density patches will especially reduce the impact of this species (Rouget et al., 2004; Gaertner et al., 2014). These virtual monocultures have been negatively associated with habitat selection of grazers and browsers (Rozen-Rechels et al., submitted); they negatively impact native vegetation through efficient competition for water and light (te Beest et al., 2013, 2015b), resulting in reduced native plant diversity (Smith, 2010) and altered invertebrate assemblages (Mgobozi et al., 2008). They also form a fire hazard when cleared, lifting ground fires into the canopy and carrying fires into areas that would normally be fire-excluding (Macdonald and Frame, 1988; te Beest et al., 2012).

This study found that fire frequency is positively related to clearing success. This is in line with previous studies that found that areas that burn frequently, such as grasslands and open woodlands, are generally more resilient to invasion (Goodall and Erasmus, 1996; te Beest et al., 2015a). Experimental work in HiP has shown that seedling establishment was much lower in burned than in unburned grassland (te Beest et al., 2015a) and grass competition was shown to be an important limiting factor for *C. odorata* performance (te Beest et al., 2013). On the contrary, rainfall was found to be negatively associated with clearing success, indicating that high rainfall areas, which are optimal habitat for the species, were more difficult to clear. Water is another important limiting factor for *C. odorata* abundance (te Beest et al., 2013) and these results suggest that a general understanding of the ecology and habitat preferences of the targeted species is fundamental to guide prioritization of clearing efforts (Nel et al., 2004). Areas with high water availability, such as riverine environments and high rainfall areas, would need prioritization and a higher intensity of clearing compared to drier areas

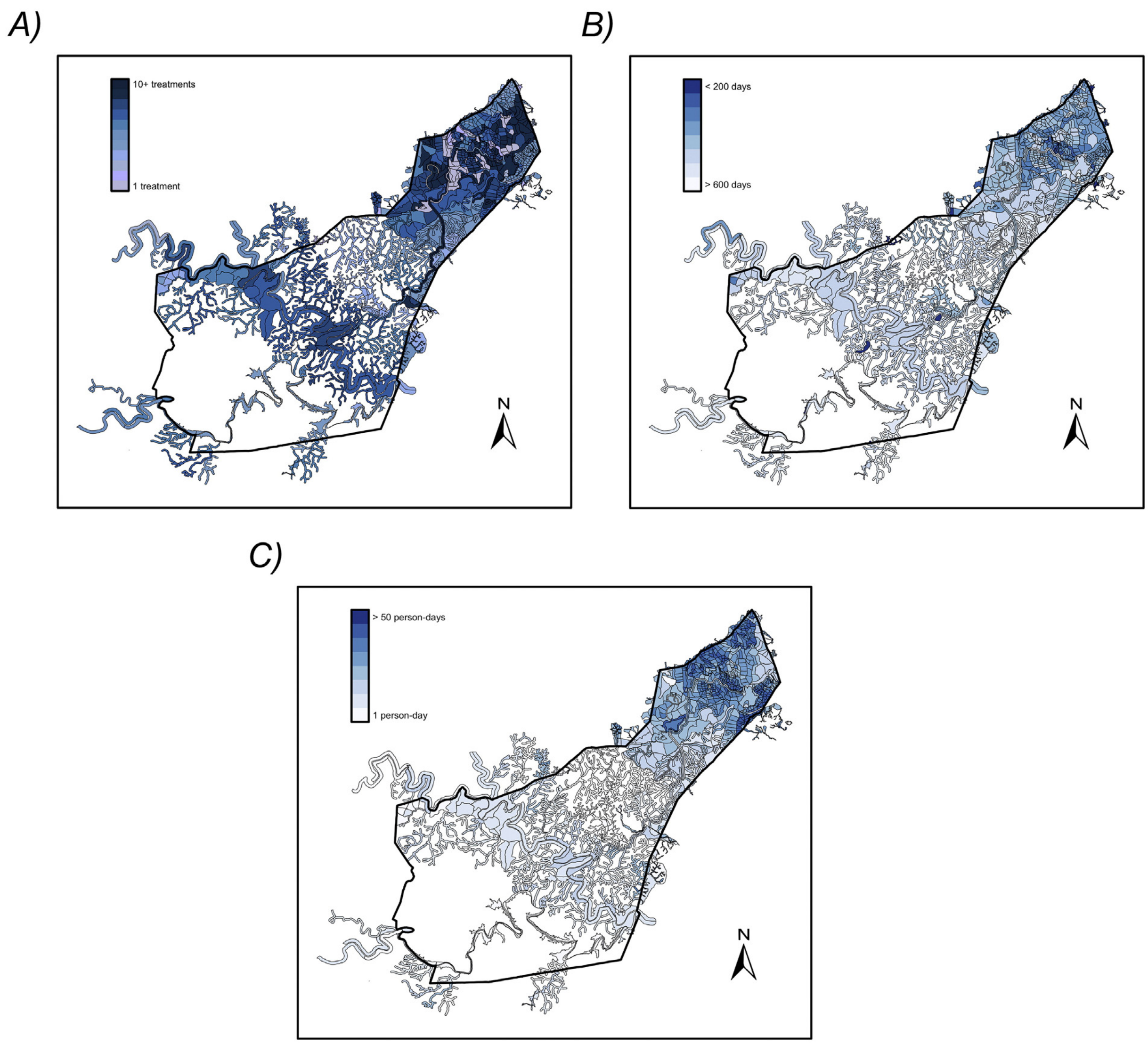

Fig. 2. Calculations based off of the Invasive Alien Species Programme of Hluhluwe-iMfolozi park during its operations from 2004 to 2014: (A) Total number of treatments per contract area. (B) Average number of days between clearing treatments per contract area. (C) Total person-days per hectare for each contract area.

(Van Wilgen et al., 2007, 2008), which was successfully done in the IASP program.

A large part of the success of *C. odorata* control in HiP can be attributed to accurate prioritization of clearing efforts in relation to fire and close collaboration between clearing operations, park management, and research. An experiment testing the efficacy of *C. odorata* control in combination with fire took place prior to and in the early phases of the rollout of the large-scale clearing program. The experiment showed that combining cut-stump treatments with fire was an effective method to control the species, but that fire alone could exacerbate the infestation, due to survival and re-sprouting of adult plants, even after intense fires (te Beest et al., 2012). Due to the fortunate timing, considerations from the experiment were incorporated into the clearing protocols from the beginning. Therefore, prioritization for clearing was given to areas that were recently burnt, i.e. clearing teams were sent in within 1 or 2 months after the fire, and fire was proven a labor-effective way to begin treatment at some sites. This is a great example of how incorporating ecological information into clearing protocols and flexibility in prioritization of control efforts increased overall clearing efficacy.

Contrary to expectation, the ecological factors minimum July temperature and maximum January temperature, were not found to be significant in the GLM model. While these parameters have been determined to be important limiting factors of *C. odorata* invasions (Raimundo et al., 2007), temperature variation within HiP may not be large enough to observe differences attributed to temperature. Also, temperature extremes are most likely not large enough in HiP to significantly inhibit *C. odorata* performance. Lower and upper temperature stress thresholds for *C. odorata* are 2 °C and 36 °C, respectively (Kriticos et al., 2005). Average minimum July temperatures in HiP range from 10.3° to 11.2 °C, and average maximum January temperatures range from 27.5 to 30.0 °C. Optimum temperatures for *C. odorata* lie between 24 °C and 30 °C (Kriticos et al., 2005). Slope and elevation were also not found to significantly affect clearing efficacy. Previous studies found positive correlations between slope, soil organic carbon, and *C. odorata* abundance in HiP (McLennon, 2006-MSc thesis), indicating either a preference of *C. odorata* for habitats with high nutrient availability, an elevated nutrient status caused by the infestations themselves, (Koutika et al., 2004; te Beest et al., 2015a), or a combination of both. It was expected that these optimal habitats would have lower clearing efficacy, similar to high-rainfall areas, but this was not found. However, elevation is confounded with both rainfall and slope in HiP and therefore the effect of rainfall could override the effects of elevation and slope. Ultimately, the increased amount of rainfall would be the factor that facilitates dense infestations of *C. odorata*, which in turn, could increase soil organic carbon.

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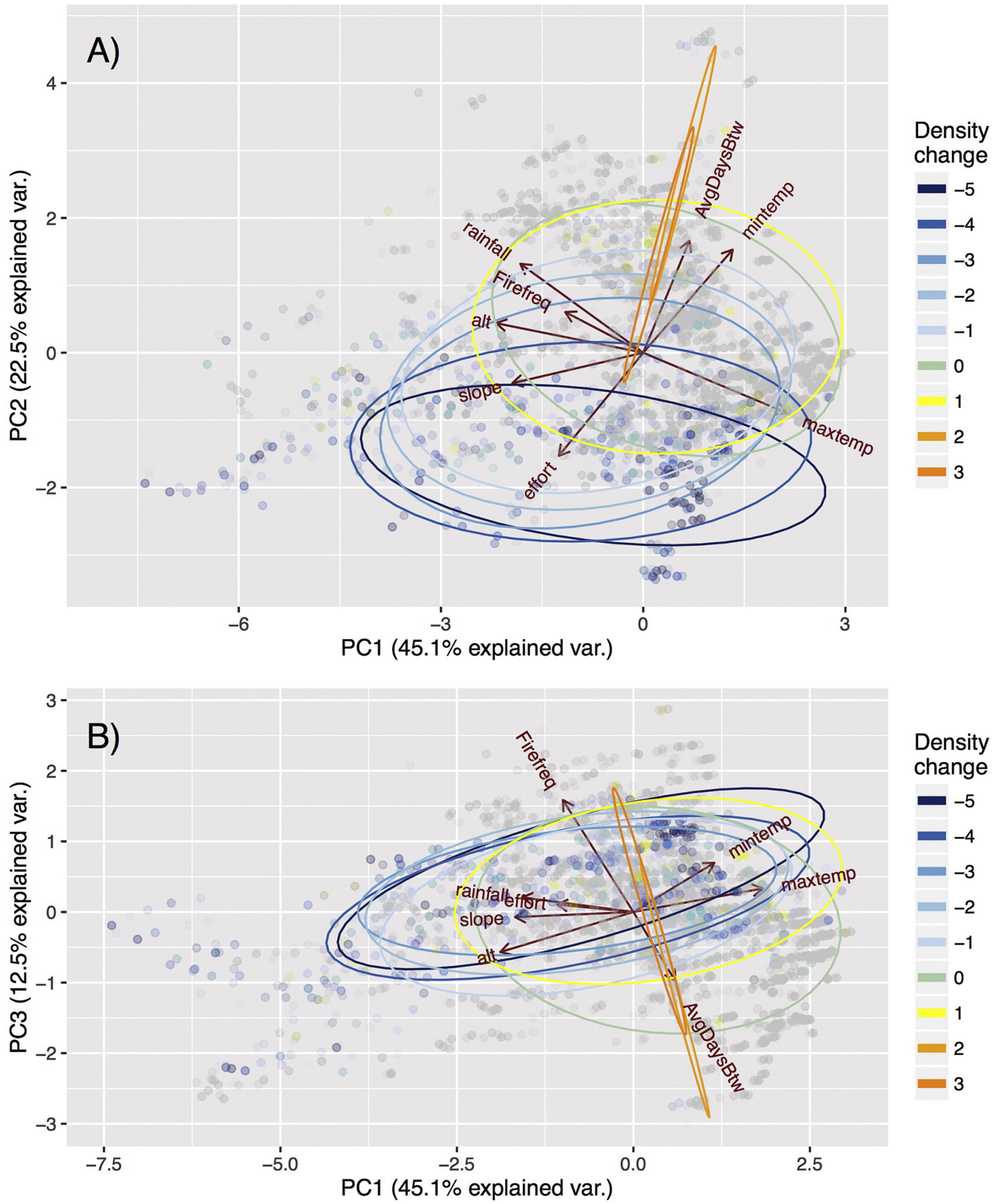

Fig. 3. PCA biplot of component 1 against component 2 (A) and component 1 against component 3 (B). Ellipses of normal probability distributions are drawn for points of each change in density class. Variables are fire frequency from 2004 to 2014 (Firefreq), average rainfall (rainfall), clearing effort, measured by the number of person-days per hectare contracted from 2004 to 2014 (effort), elevation (alt), slope (slope), average maximum temperature in January (maxtemp), average minimum temperature in July (mintemp), and average days between each clearing treatment (AvgDaysBtw).

Effort has had the strongest positive effect on clearing efficacy, according to the GLM analysis. The *C. odorata* invasion in HiP has gone from the northern section of the park being 20% covered in dense infestations in the early 2000s (Howison, 2009-MSc thesis) to virtually no dense patches detected in transect sampling in 2014. Unfortunately, applying the effort that was necessary to reduce the density of *C. odorata* in HiP to such a degree involved a great amount of manpower and large financial inputs, neither of which are readily available to any land manager (Van Wilgen et al., 2016). Nevertheless, the poverty-relief structure of programs like Working for Water and the Invasive Alien Species Programme of HiP are a great model for providing the resources and manpower necessary to combat invasive species (Turpie et al., 2008), and there is great potential to apply this model in other regions of the world, simultaneously reducing poverty and providing the workforce needed to combat biological invasions.

The average amount of days between clearing treatments was not associated with clearing efficacy in this study. Longer periods between clearing events could result in lower efficacy and greater cost per hectare if the invader is allowed to grow back to previous densities (Marais and Wannenburgh, 2008). In HiP the IASP prioritized follow-up clearing treatments only when an area was considered to be in need of clearing, instead of following up after a pre-determined period (C. Terblanche, pers. comm.). Not having standardized periods for follow up increased flexibility in planning and allowed for accurate response to actual densities: longer periods for low densities and shorter periods for high densities. If this strategy works well, both longer and

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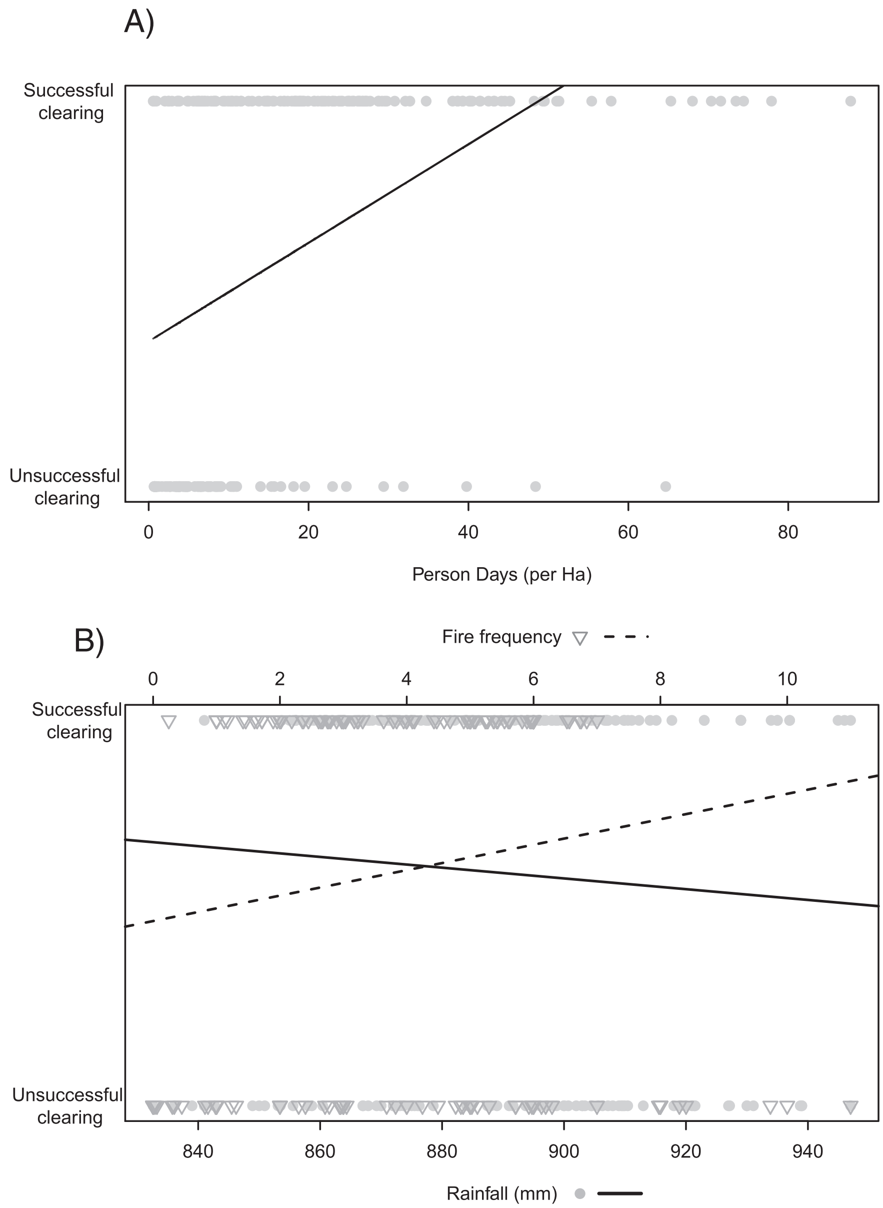

Fig. 4. (A) Clearing success vs. effort. Effort is measured in person days per ha contracted to each clearing area from 2004 to 2014. The minimum effort contracted was 0.5 person days per hectare. (B) Clearing success vs. rainfall (bottom, solid line) and fire frequency (top, dashed line). Rainfall is the average rainfall of HiP, sourced from the WorldClim database, and fire frequency is the frequency from 2004 to 2014 of fires in HiP.

shorter periods would have equal clearing efficacy, which is exactly what was found in this study. This shows that the strategy followed by the IASP, linking follow-up clearings to actual densities, has worked well, provided that it is performed in combination with regular density assessments.

A considerable amount of seasonal variation was found in clearing efficacy. For the main clearing method, cut-stump treatment, clearing efficacy was highest in the wet season and the main flowering season (June–July). A rapid decline in clearing efficacy occurred from July to August, coinciding with the seed drop of *C. odorata* in August and September. Disturbance during this period can leave conditions optimal for the establishment of *C. odorata* seedlings (te Beest et al., 2012). The decrease in clearing efficacy in May and December is less clear. May clearings could be less successful due to the coinciding start of the dry season, when plants withdraw nutrients into their basal stems, which render them less sensitive to aboveground disturbances. In November/December a second flowering/seedset event usually occurs when conditions are optimal that might explain the decline in clearing efficacy. However, non-ecological factors might also play a role. May is also the beginning of the fiscal year and could incur some changes in clearing quality due to budget and training. December is a holiday month when work is often scaled down and many tourists visit the park, which could increase the spread of seeds. Blackmore (1998) showed that mature seeds can travel very far in the tires and bodywork of vehicles. Therefore, it may be best to halt clearing during the months of August and September, not only to reduce disturbance at the clearing sites during seed dispersal, but also to ensure that seeds do not get spread to other areas through the medium of boots, clothes, and cars. Clearing activity should be increased during June and July to clear plants when they are most vulnerable during flowering, and to clear a stand before new seeds mature.

The results of this study have offered insights into the successes of the clearing program in HiP and underline the importance of ongoing invasive alien plant monitoring. Now that densities in the park are

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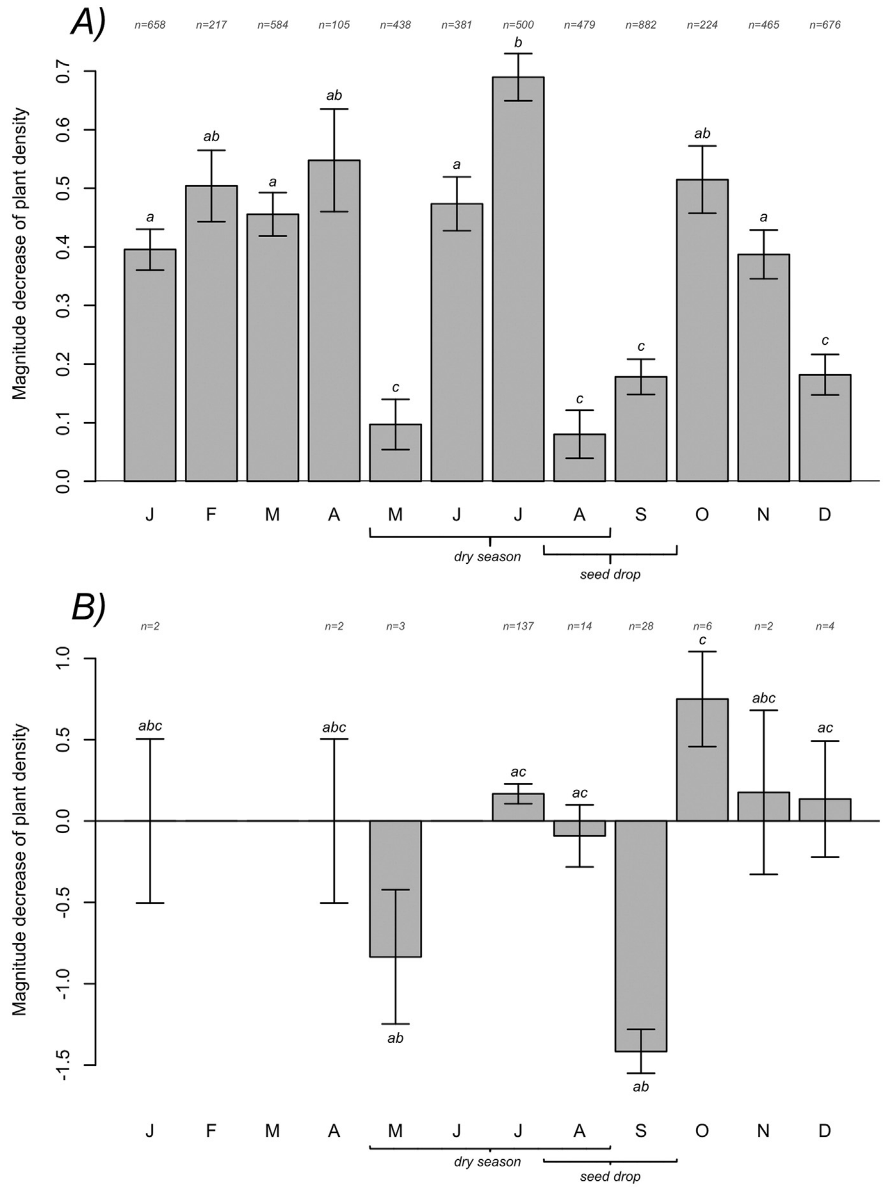

Fig. 5. Mean log density decrease of *Chromolaena odorata* for each clearing contract area by treatment month from one treatment to the following by treatment method: (A) cut-stump treatment, (B) hand-pulling.

lower, management may need to be reformed and more focus given to monitoring instead of eradication, especially considering that on three of the twenty-four transects densities slightly increased between 2010 and 2014 (Table 2). Early detection and rapid response are valuable tools to prevent reinvasion in a cost-effective manner (Myers et al., 2000). The history of HiP shows that an introduced species can go from first appearance to an aggressive invasion in a period of a mere 30 years. For that reason, it will be important to establish a cost-effective monitoring system that can be utilized continuously, even during budget shortages and in periods where invasions do not seem as threatening. For example, incorporating the monitoring methods used in the current study into the biennial game census transects could be very beneficial and cost-effective. Alternatively, developing an invasive plant reporting system for field rangers similar to methods used in Kruger National Park (Foxcroft et al., 2009) could be valuable. These approaches could give the park enough preliminary data to take proactive measures against the rise or resurfacing of invasive plant species in HiP, which could be very important, as the most cost-effective management of invasions is still prevention (Simberloff, 2009).

This study shows that clearing programs could save time and resources by including seasonal planning, incorporating fire where possible, and taking ecological factors into account during prioritization. Gathering data of plant invasions both before and during management actions can give very important ecological information for the management of these species (Blossey, 1999), and Hluhluwe-iMfolozi Park is fortunate to have such data. The amount of effort employed per contract area had the strongest relationship to clearing efficacy. This is an important outcome that highlights that when large effort is applied, clearing can be successful, despite other factors affecting clearing efficacy. It is noteworthy that the IASP in Hluhluwe-iMfolozi Park followed standard WfW protocols that proved instrumental in its success, but the IASP had the additional benefit of working with only one landowner, which made it easier to be flexible in planning and incorporate the use of fire. Decisions from management or land-owners can have a large impact on the results of a clearing program, which is what greatly complicates invasive species management at a national scale. Nevertheless, the successes and setbacks of managing *C. odorata* in HiP could provide important lessons to facilitate invasive alien plant management in other areas or countries, and especially be an aid to those with fewer disposable resources.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.sajb.2016.12.007.

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