Master thesis – SUSD ECE

The response of 6 alien invasive plant species to spatiotemporal variations in water availability in Hluhluwe iMfolozi park

Kas Jansen (6313426)
k.jansen5@students.uu.nl

Supervisor: Mariska Te Beest
Second reader: Jerry van Dijk
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Abstract

Humans are one of the largest contributors to current global biological invasions, spreading species across the globe. Biological invasions are characterized by species being transported from their native range to new locations, where they start to spread uncontrollably due to both biotic and abiotic drivers. The impacts of biological invasions in South Africa are not limited to issues regarding ecological degradation, but also inflict economic implications and water scarcity problems. In HiP 6 species are identified as the most widely spread alien invasive species: *Chromolaena odorata, Parthenium hysterophorus, Lantana camara, Tagetes minuta Opuntia ficus-indica, and Opuntia aurantiaca.* The invasive species have different strategies when it comes to coping with water availability. The aim of this study is to monitor the distribution and density of 6 alien invasive plant species in HiP, and to increase our understanding on how climate change affects the alien invasive plants in regard to their strategy, in terms of variability in spatial and temporal water availability. We found that all the observerd alien invasive species have significantly increased in 2019. Also, that most of the invasive species are found in Manzibomvu, the section with the most rainfall. These findings seem to agree with the trends in spatial and temporal water availability. They also seem to relate to the practises of the WfW programme, notably the hold up of it in 2016, especially for *C. odorata*. *C. odorata* has increased the most in 2019 and is still the most abundant invasive species in HiP.

Preface

Before you lies a research about the response of 6 alien invasive plant species to variations in spatiotemporal water availability in Hluhluwe iMfolozi park. This research was carried out as a graduation thesis to fulfil graduation requirements of the master program "Sustainable Development – Environmental Change and Ecosystem" for Utrecht University, from November 2018 until July 2019.

Part of the research involved doing data collection in South-Africa, which I am very grateful for. I would like to thank my supervisor for this opportunity and the guidance and support during this process. Also, I want to thank Phumlani, the research assistant who helped collecting data in the field and Falaka, the game guard who kept us safe while walking the transect. I want to thank everyone that helped me with my project.

Introduction

Humans are one of the largest contributors to current global biological invasions, spreading species across the globe. As we are living in an era where globalization dictates the rules of the game, the magnitude of biological invasions is only expected to increase (Hulme, 2009; Vitousek, et al., 2017). Biological invasions are characterized by species being transported from their native range to new locations, where they start to spread uncontrollably due to both biotic and abiotic drivers (Mack et al., 2000; Diez et al., 2012). Abiotic drivers may facilitate biological invasions, for example through the occurrence of extreme climatic events (ECEs) that are increasing with ongoing climate change. Increasing ECEs have influence on each phase of the invasion process, from the introduction and the establishment phase, through the spread and impact phase. It does so by facilitating transport of propagules to new areas, decreasing resistance of native communities to establishment of the invasive species, and by stressing and disturbing the native community (Diez, et al., 2012).

Biological invasions have the potential of degrading native species diversity, and is considered the second largest cause of biodiversity loss (Vitousek, et al., 1997). The impacts of invasive species vary in magnitude and severity. Where some invasions have no substantial impact on ecosystems and only cause alterations on the community level, other invasions cause regime shifts (Gaertner et al. 2014) and dismantle the fundamental structure of an ecosystem (Jeschke et al., 2014). Invasive plant species may cause these alternations by utilizing excessive amounts of water, light and oxygen, by adding resources, facilitating or suppressing fire, holding sand or contributing to erosion, accumulating litter and by accumulation or the redistribution of sand, resulting in altered nutrition flows (Richardson, 2004).

Plant invasions in South Africa

South Africa is home to an extraordinary variety of plant species and has the richest temperate flora in the world. South Africa is home to more than 10% of the world's vascular plant flora, that is approximately 24,000 species in 368 families (Germishuizen & Meyer, 2003). During colonial times, by accident or for agricultural purposes**,** approximately 750 tree species and 8000 shrubby, succulent and herbaceous species have been introduced to South Africa; 161 of these species (38 herbaceous, 13 succulent and 110 woody) are considered severely invasive, and many more are expected to become weeds in the future (Van Wilgen, et al., 2001). Data extracted from the South African Plant Invaders Atlas (SAPIA) (Henderson, 1998) allowed Richardson and Van Wilgen (2004) to compose a map illustrating the distribution of 180 invasive plant species in South Africa (fig 1). In totality these invasive plants cover ten million hectares of South Africa, the largest amount of invasive plants are found along the eastern coast and in the western Cape. (Richardson & van Wilgen, 2004).

The impacts of biological invasions in South Africa are not limited to issues regarding ecological degradation, but also inflict economic implications and water scarcity problems. The removal of invasive plant species is an expensive venture. The total costs to bring the alien invasive plant species under control in South Africa is estimated to a total of 1.2 billion US dollars (Van Wilgen, 2001). In addition, South Africa is a water-stressed nation, and water scarcity is considered as the greatest and most urgent holdback for further development for South Africa (Turpie, 2008). Biological invasions contribute greatly to South Africa's water scarcity. Van Wilgen (2008) shows that invasive plant species reduce the surface water runoff with 7% of the South Africa's total water runoff. As a response to the threat of developing further water scarcity the Working for Water programme (WfW) was initiated in 1995. This initiative aimed to remove alien invasive plants in order to decrease the threat of water scarcity, and to further improve the ecological conservation efforts (Dew, et al., 2017; van Wilgen, 1998). The WfW programme receives subsidies from the government's poverty relief budget with the aim of decreasing unemployment, while at the same time reducing the problem of alien invasive plants (van Wilgen, et al., 2001).

Climate change further complicates the issue of biological invasions. South Africa is warming in a consistent pace and over the next 20-40 years in a mild scenario an increase of 1-2.5 degrees Celsius is expected (van Wilgen, 2016). By 2100 temperatures in the northwest could reach up to 5.5 degrees, and in more conventional scenarios up to 7.5 degrees. The south west and central west could reach up to 4.5 degrees. In addition, more frequent hot extremes and an increase of seasonal rainfall with longer and drier periods are expected, potentially leading to an increase in extreme flooding as well as drought events (van Wilgen, 2016). During 2015-2016 most of South Africa experienced a severe drought event and there is a pressing need to understand how invasive plant species will respond to climate change, notably to changes in water availability. Furthermore, Richardson (2004) expresses that there is a need for more data about the distribution and density of alien invasive plant species in South Africa to gain more insight in the current ecological state of South Africa's ecosystems and biodiversity.

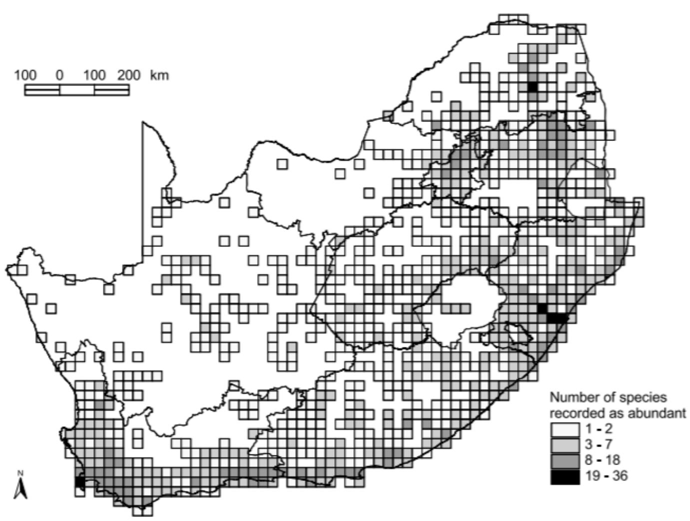


Figure 1 map illustrating the distribution of 180 invasive plant species covered over 10 million hectares in South Africa (Richardson & van Wilgen, 2004)

Invasive plant species of HiP

In HiP 6 species are identified as the most widely spread alien invasive species: *Chromolaena odorata, Parthenium hysterophorus, Lantana camara, Tagetes minuta Opuntia ficus-indica, and Opuntia aurantiaca.* In this study the main focus is on the most widely spread invasive species *C.* odorata, the other 5 species will be referred to as priority species. The invasive species have different strategies when it comes to coping with water availability. Field observations of the shrub *C. odorata* show that periods of high rainfall are beneficial to establishment, the species is however restricted to riverbanks in drier areas (Te Beest et al. 2013; Dew et al. 2017). In general, *C. odorata* is a highly competitive species, but in order to outcompete other plants it needs a disturbance to gain the upper-hand (Te Beest et al. 2013, 2015a). The bushes are about 1.5-2 m in height and can reach up to 6 m when grown on top of other plants (Te Beest, et al., 2009). It originates from the south and central Americas, and was first recorded as native in the 1940s in Durban, South Africa (Zachariades & Goodall, 2002). The plant is known to affect indigenous forests and savannas. The WfW has been focusing primarily on *C. odorata* in HiP, as it is the most severe invasive species in the park. As of 2004 the park started to collect data about the density and distribution of the species. In 2016 the WfW put the removal of *C. odarata* to a hold, due to an accident with one of the employees in the park.

P. hysterophorus is a ruderal plant species with an annual life history and very tolerant to disturbances and droughts. It is able to grow in all sorts of soil types and in a wide range of moisture and temperature conditions, it does however need high soil moisture for seed germination (Gnanavel, 2013). The plant is native to the Americas and the West Indies, and is considered to be one of the worst weeds currently known. It is known to inflict issues regarding biodiversity, ecosystems, human and animal health implications, such as dermatitis, asthma and bronchitis, and agricultural losses (Kaur et al., 2014).

Tagetes minuta is also a ruderal with an annual life history. It is drought resistant and can tolerate high temperatures and periods of low rainfall. It can grow in dry and in moist soils (SANBI, 2019). The plant is native to South America and is known for its strong odour. In South Africa the crop is known to infect the agricultural land, as the dry weight and height of the crops planted in previously infested *T. minuta* soil were significantly reduced (Holm et al., 1997).

Lantana camara is a highly competitive shrub and thrives in a variety of soil types in which soil moisture is available, but it is also known to be able to tolerate long periods of droughts (Gunasekara, 2017). It is considered a notorious weed, it is a woody straggling plant with various flower colours. *L camara* is a shrub native to tropical and subtropical America, and has been introduced in South Africa from Natal by birds. The plant is aggressive and an outbreeder weed that has settled and is dominant in vast expanses of pastures. The plant is known to grow at altitudes up to 2000m in tropical and temperate regions (Ghisalberti, 2000).

The two cacti, *Opuntia fiscus-indica* and *Opuntia aurantiaca* can tolerate low water availability to a great extent, typically for a cactus species. These species are very stress-tolerant and mostly found in arid areas. The plants are native to middle and North America (Johnson & Stiling 1996).

Using the CSR model, further elaborated upon in the theoretical background chapter, the strategies of the invasive plant species of HiP can be divided into the three different categories (table 1).

Chromolaena odorata	Competitor
Lantana camara	Competitor
Parthenium hysterophorus	Ruderal
Tagetes minuta	Ruderal
Opuntia ficus-indica	Stress tolerant
Opuntia aurantiaca	Stress tolerant

Tabel 1 Invasive species in CSR model

Research aim

The aim of this study is to monitor the distribution and density of 6 alien invasive plant species in HiP, and to increase our understanding on how climate change affects the alien invasive plants in regard to their strategy, in terms of variability in spatial and temporal water availability. To this end we will measure the distribution and density of 6 alien invasive plant species, most notably *C. odorata*, in HiP that differ in their ability to cope with periods of low water availability and compare the current distribution and density data to previous monitoring data (2004-current for *C. odorata* and 2014-current for the other 5 species). In this way this thesis simultaneously contributes to the monitoring of alien invasive plant species in HiP. The following research question and sub-questions are proposed:

How does spatial and temporal variation in water availability affect the distribution and density of 6 alien invasive plant species in HiP?

- *What is the spatial and temporal variation in water availability in HiP?*
- *What is the distribution and density of the most widespread invader, C. odorata, in HiP in relation to the water availability in space and in time?*
- *What is the distribution and density of 5 priority invaders in HiP in relation to the water availability in space and in time?*
- *Do the 6 invasive plants have different strategies to cope with the temporal and spatial variation in water availability in HiP?*

Hypotheses

Stress tolerant plant species, such as *Opuntia* sp., are likely to do well in arid areas. It is expected that a drought event will not have a significant impact on their distribution and density. It is expected that *O. ficus-indica* will generally be found in the southern part of HiP, this is due to the high tolerance to low water availability of cactus species. Competitive plant species, such as the shrubs *C. odorata* and *L. camara* might be affected by a drought event initially and therefore decrease in numbers. *C. odorata* is most likely to increase relative to the pre-drought distribution and density, especially in the northern part of HiP and close to rivers. *L. camara* is expected to be more abundant in the southern part of HiP. However, after the drought event their numbers are likely to increase relative to the pre-drought density and distribution due to their higher growth rates as compared to native species (te Beest et al. 2015b). The ruderals are expected to do well during a drought event, as they have favourable traits when it comes to sudden changes. The highest abundance of *P. hysterophorus* and *T. minuta* are likely to be found in the northern part of HiP.

Theoretical background

Invasion process and climate change

Upon arrival in the new area many obstacles are imposed for the alien species, which has to adapt to the conditions of the new environment. This is the first phase of the invasion process that consists of four phases which an alien invasive species goes through when settling in a new area. (i) The transport stage, in which a species is introduced to a specific area. (ii) The establishment stage, in which biotic resistance of native species can be reduced due to disturbances and stressors. (iii) The spread stage, the species has overcome the dispersal barriers and is able to settle in the specific area. (iv) The impact stage, in which invasive species may have the upper-hand if they have superior resistance to the climatic conditions, opposed to their native competitors (Diez et al., 2012).

According to Diez (2012) extreme climatic events (ECEs) influence all the stages of the invasion process, and have the potential of accelerating the invasion process and increasing the net result of invasive plant species. ECEs such as storms influence the transportation phase by facilitating transport for seedlings and by the increasing the distribution rate of invasive plant species. Winds and storm surges may influence movements of a species and can trigger large scale immigration. In the establishment phase ECEs may cause disturbances for the native plant species and ECEs may stress native plant species, increasing the physical resources availability for invasive plants. In addition, ECEs dilapidate the biotic competition, which is favorable for the spread and dispersal rate of the invasive species. In the impact phase invasive species might prove to be more resistant to ECE than its competitors, and increase the probability of fire events for example (Diez et al., 2012). Drought events have the most critical influence on the establishment, spread and impact phase. Droughts increase the probability of fire events, and alter the physio ecological composition of ecosystems, with the potential of creating a more favorable environment for invasive species. In addition, droughts cause limitations in resource availability such as water, and thus disturb the routine resource depletion of native plant species. Plants with effective traits that endure such changes, can prevail their competitors.

Plant strategies

The success of a plant while adapting to its continuously changing climate depends on three determinants: competition, stress and disturbance. When multiple plants settle in the same physical environment, they are forced to share the available light, water, nutrients and space. Each plant will rival for its share of resources, this plant interaction is described as competition. The stress determinant relates to the physical environment, which depends on availability of resources (e.g. light, water, nutrients). Disturbances relate to physical damage to the vegetation (e.g. grazing or soil erosion). Stress and disturbances have influence on the magnitude of competition, as they can impose physical barriers or not, and determine resource availability.

In the process of adapting to one's environment, plants have developed traits in order to cope with competition, stress and disturbances. The traits important for competing with other plants focus on efficient resource capture and utilization. Elevated leaf canopy, extensive ability to spread below and above ground, and a thick layer of litter on the ground surface are traits that are important in a competition strategy. An important attribute for the stress tolerant strategy seems to be a small stature and a low potential relative growth rate, this seems to hold up when settled on acid soils, low shade areas, and desiccation. An important characteristic of the disturbance strategy relates to dispersion, when under stress the plant prioritizes seed production over biomass growth (Grime, 1974).

Competitors are usually found in areas that have low intensities of stress an disturbances and outcompete other plants by efficiently using the available resources. They rely on characteristics that maximise the capture of resources in productive relatively undisturbed conditions. Such as rapid growth rate and high productivity. The morphology of competitors are usually herbs, shrubs and trees, with a high dense canopy of leaves, which are robust and often mesomorphic. Stress tolerant species are found in areas with high stress intensities and low disturbance intensities and can endure in continuously unproductive environments, they are characterised by slow growth rates. The morphology are usually lichens, herbs, shrubs and trees with and extremely wide range of growth forms. The leaves are often small or leathery, or needle-like. The ruderals are found in areas of high intensity disturbances and low intensity stress. They have a short life cycle and are often annuals. Ruderals are mostly herbs with small stature and limited lateral spread (Grime, 2006).

Methods

The distribution and density of the 6 invasive plant species in Hluhluwe-iMfolozu Park have to be mapped and studied in order to learn more about the effect of the water availability on the plant species. How this is done exactly is further elaborated upon in the following chapters.

Study area

The Hluhluwe iMfolozi park is located between 28°00′–28°26′ S and 31°43′–32°09′ E in northern KwaZulu-Natal Province, South Africa (fig. 2). The park is 90,000 ha and comprises out of 3 parts; Hluhluwe Game Reserve, iMfolozi Game Reserve, and the conservation corridor. It is a hilly region and elevation ranges from 60 to approximately 600 m above sea level, with higher altitudes in the north than the south.

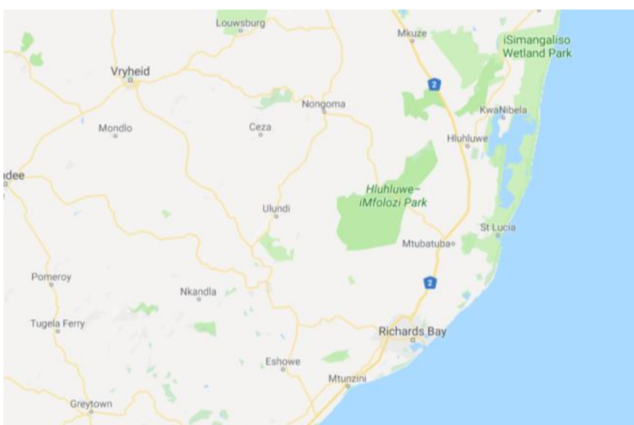


Figure 2 provincial map of Hluhluwe-iMfolozi Park

Water availability in HiP

Hluhluwe-iMfolozi Park (HiP) is a nature reserve located in the east of South Africa. In this area rainfall is strongly seasonal, with most rain falling from October to March (Balfour & Howison, 2002). There are is a strong rainfall gradient (fig 3), with around 1000 mm annually in the northern part and 600 mm in the southern part (Dew, et al., 2017; Boundja & Midgley, 2010; Balfour & Howison, 2002). During 2015-2016 the Eastern parts of South Africa experienced a severe drought.

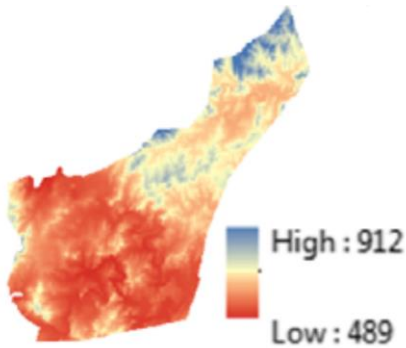


Figure 3 Annual rainfall in Hluhluwe iMfolozi Park in mm (Veldhuis et al., 2017).

Data collection

The distribution and densities of the alien invasive plant species were recorded for 2004, 2010, 2014 and 2016 for 25 different transect scattered across the park. The transects are displayed in figure 4, the dashed lines indicate uncut transects, and the solid lines indicate cut transects. HiP has 25 cut line-transects across the park and an additional 8 uncut transects, initially these transects were intended to analyse animal populations. However, these transects have been used to collect data about the distribution and density of alien invasive species since 2004 and will be used for the data collection of 2019 as well.

The park is divided into 5 sections, Manzibomvu, Nqumeni, Masinda, Mbuzane and Makhamisa (Fig. 4). Each of these sections contain several transects that will be included in this analysis. The Makhamisa section will be excluded, as all of those transects are in the wilderness and are uncut, making them very complicated to reach. In addition, in 2019 transect 13, 14 and 17 are excluded due to high river levels, making it too risky to cross the river intercepting the transects. In table 2 the sections with their corresponding transects and mean annual rainfall are described. Each section has different environmental conditions, the Manzibomvu and Nqumeni sections are located in the more elevated 'wet' areas, and the Masinda and Mbuzane sections are located in the lower lying 'dry' areas.

Figure 4 Map displaying the north part (white) and the south part (Grey), and the cut (solid lines) and uncut(dashed lines) transects in Hluhluwe iMfolozi park

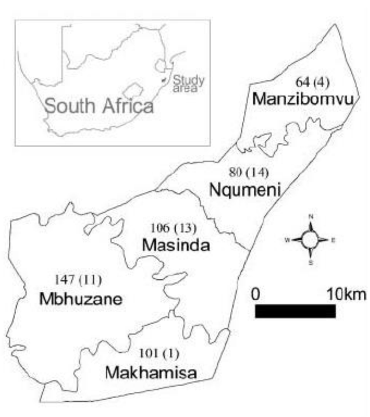


Figure 5 map illustrating the 5 sections of HiPReid, C., et al (2007)

Section	Transect	Mean annual rainfall
Manzibomvu	1-5	746.47
Nqumeni	6-12	619.35
Masinda	15-18	374.58
Mbuzane	13-18, 21-26	362.20

Table 2 Sections of HiP with their respective transects and their respective mean annual rainfall.

The plant distribution and density will be recorded using the same collection method as previous invasive species inventories in the park, using cover estimates for 5x2m blocks on a 5-point scale, which is based on a modified Braun Blanquet (1932) scale. Our modified scale gives an indication of the plant cover using the following categories (Table 2):

0	No plant cover
1	Cover of <5% (few individuals present)
2	Plant cover 5-25%
3	Plant cover 25-50%
4	Plant cover 50-75%
5	Plant cover >75%

Table 2 plant cover indication scale

In order for the records to reflect the actual plant density and distribution for each transect, an cover estimation will be done for a 5x1m plot on each side of the transect every 5m along the respective transect. In this manner the final data will display an accurate reflection of the alien invasive plant distribution and densities along the transects. In addition, this data collection will take place in January-April, other than previous alien invasive plant species data collection activities in HiP, which took place in the time period October-December.

Available data

The first data collection for invasive plant species is done in October-December 2004. This was data collection for the distribution and density of only *C. odorata*, and was done in 50x2m plots rather than 5x2m plots as used in succeeding years. Every 50m an estimation was made for a 50x1m plot to the right and to the left of the transect. In October-December 2010 the distribution and density for only *C. odorata* was collected. The data was collected for 5x1m plots for the left and for the right side of the transect. In October–December 2014 the distribution and density of 8 alien invasive plant species was collected for 23 transects in HiP. The survey included the following species: *C. odorata, L. camara, Solanum mauritianum, P. hysterophorus, Opuntia spp., Melia azedarach, T. minuta* and *Campuloclinium macrocephalum*. No or few records were found for *S. mauritianum, M. azedarach* and *C. macrocephalum*, therefore they were not included in subsequent surveys. Every 5m an estimation was made for 5x1m plot to the left and the right of the transect. During this year the WfW programme was still clearing *C. odorata* from HiP, therefore it should be considered that changes in *C. odorata* densities may also be the consequence of the removal practices of WfW.October-December 2016, at the height of the drought, a survey of 5 alien invasive species was conducted, including the following species: *C. odorata, P. hysterophorus, L. camara, T. minuta and Opuntia spp.*. The inventory was conducted along the same 23 transects in HiP. Every 5m an estimation was made for 5x1m plot to the left and the right of the transect. During this year the WfW programme stopped with the removal of *C. odorata*, therefore it should be considered that an increase in *C. odorata* may also be caused by the discontinuation of removal practices from WfW.

HiP has detailed rainfall records going back to 1955, as well as GIS layers with information about long-term rainfall patterns, rivers and distance to water as well as a Digital Elevation Map, slope and altitude. Each section has several measurement stations collecting rainfall data.

Data analysis

The data allows for two different analysis, one focussing on the *C. odorata* distribution from 2004-2019, and the other one focussing on all the species distribution from 2014-2019. In order to work with the *C. odorata* data it has to be converted to the same format. In 2010 an estimation for the whole plot was made, rather than a division between the cover estimation on the left and right of the transect. The maximum of the left and right of each plot was taken for the data from 2004, 2014, 2016 and 2019, to represent the density of the transects. The 2004 data is collected for 50m plots, whereas the data for the succeeding years have been collected for 5m plots. This data has to be converted in order to analyse it and that is done using different methods for each data set, this is elaborated upon below.

Presence/Absence

The Presence/Absence (P/A) describes the distribution of the species along the transects. The value for *C. odorata* is converted in two ways. 1) For each transect of the years 2010, 2014, 2016 and 2019, there is either a minimum of 1 invasive plant species in a 50m plot or no invasive plant species. If there is a presence of *C. odorata* in a 50m plot, this plot is marked as 1. If there is an absence in this plot the plot will be marked as 0. The percentage of the ‘presence’ plots is calculated for the whole transect. Resulting in an actual resolution Presence/Absence value for each transect. 2) For each transect there is either a minimum of 1 invasive plant species per 50m or 5m plot, or there is no invasive species. If there is a presence in a plot it is marked as a 1, if there is an absence this plot as a 0. The percentage of the ‘presence’ plots is calculated for the whole transect, and gives a P/A value for the whole transect.

The P/A for all the invasive species only includes data from 2014-2019. For each transect there is either a minimum of 1 invasive plant species per 5m plot, or there is none. The plots in which there is a presence are marked as 1, the ones where there is none are marked with 0.The percentage of the ‘presence’ plots is calculated for the whole transect, and gives a P/A value for the whole transect.

Cover average percentage

The cover average percentage describes the density of the species for each transect. It is calculated by transforming the 1-5 scale to a 0-100 scale (according to table 2). The percentage of cover is calculated for each transect, resulting in a cover average percentage value for each transect.

Rain fall data

The total rainfall for each section in the years 2004, 2010, 2014, 2016 and 2019 is calculated. In addition the total park average rainfall data is calculated for each year.

Data transformation

In order to meet the assumptions of normality, the data is transformed from percentages. The most compatible transformation formula is decided upon by visually inspecting Q-Q plots and running a Shapiro test (Appendix **X**). The following transformation formula was used:

LOG(y+1)

Analysis
In order to visualize the temporal and spatial effect GIS is used to create maps that demonstrate the distribution and density of all the species in HiP over the years with available data.

The rainfall data from 2004-2019 shows the water availability in relation to the alien invasive plant species over time and how it is distributed across the park. The yearly rainfall will be used as a proxy for the variations in temporal water availability, and the section rainfall will be used as a proxy for variations in spatial water availability.

The analysis are done by running 2 general linear models for C. odorata, the 5 priority species and the CRS groups separately, with the LOG transformed dependent variables; Presence/Absence and the average cover percentage. The fixed factors will include both the spatial and temporal variation in water availability. The fixed factor Year is used as a proxy for variations in temporal water availability, and Section is used as a proxy for variations in spatial water availability. In addition a post-hoc S-N-K test is run for Year*Section.

Results

The spatial and temporal rainfall distribution
Figure 6 indicates that the northern sections receive the most annual rainfall,. In 2014 the rainfall levels are relatively low. This was the start of a major drought that lasted until January 2017 (Staver, et al., 2019)

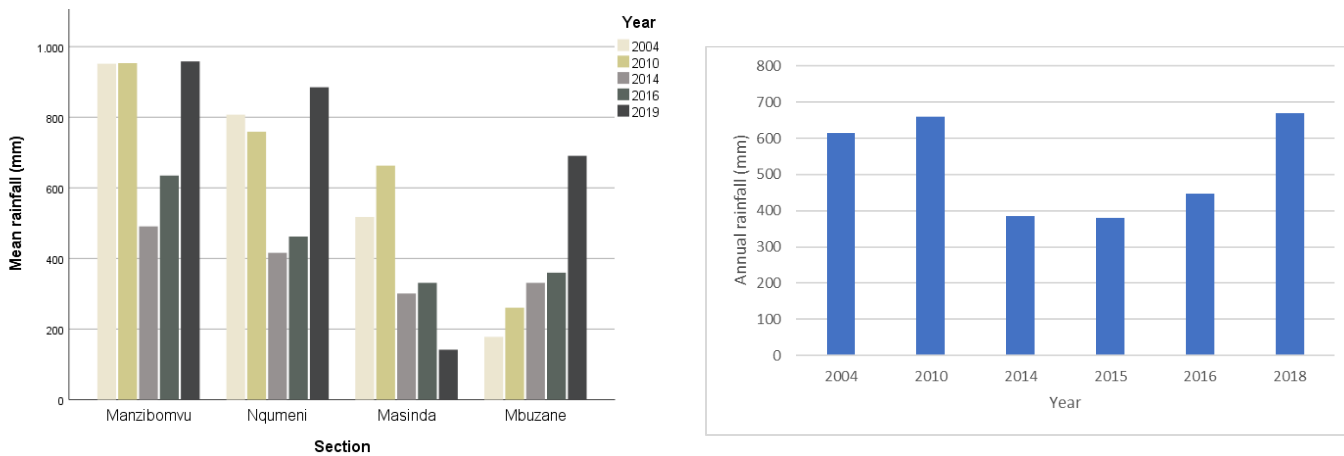


Figure 4 Spatial and temporal rainfall distribution in HiP from 2004-2019, in the sections Manzibombu, Nqumeni, Masinda and Mbuzane. The sections are ordered by amount of rainfall, descending from highest to lowest, and also from north to south, see also figure 2.

The effect of spatiotemporal water availability on the distriution and density of C. odorata
In figure 7 the distribution and density of *C. odorata* in HiP is displayed. The years 2004-2016 show that the amount of *C. odorata* s decreasing in the region. This corresponds with the practices of WfW, that started in 2004 and stopped in 2016. In 2019 an increase of the invasive species compared to 2010-2016 is seen. Also, a clear division between the northern and the southern part is shown, where in the northern part there is significantly more *C. odorata* than in the southern part. The highest density of *C. odorata* can be seen on transect 1,2 and 3.

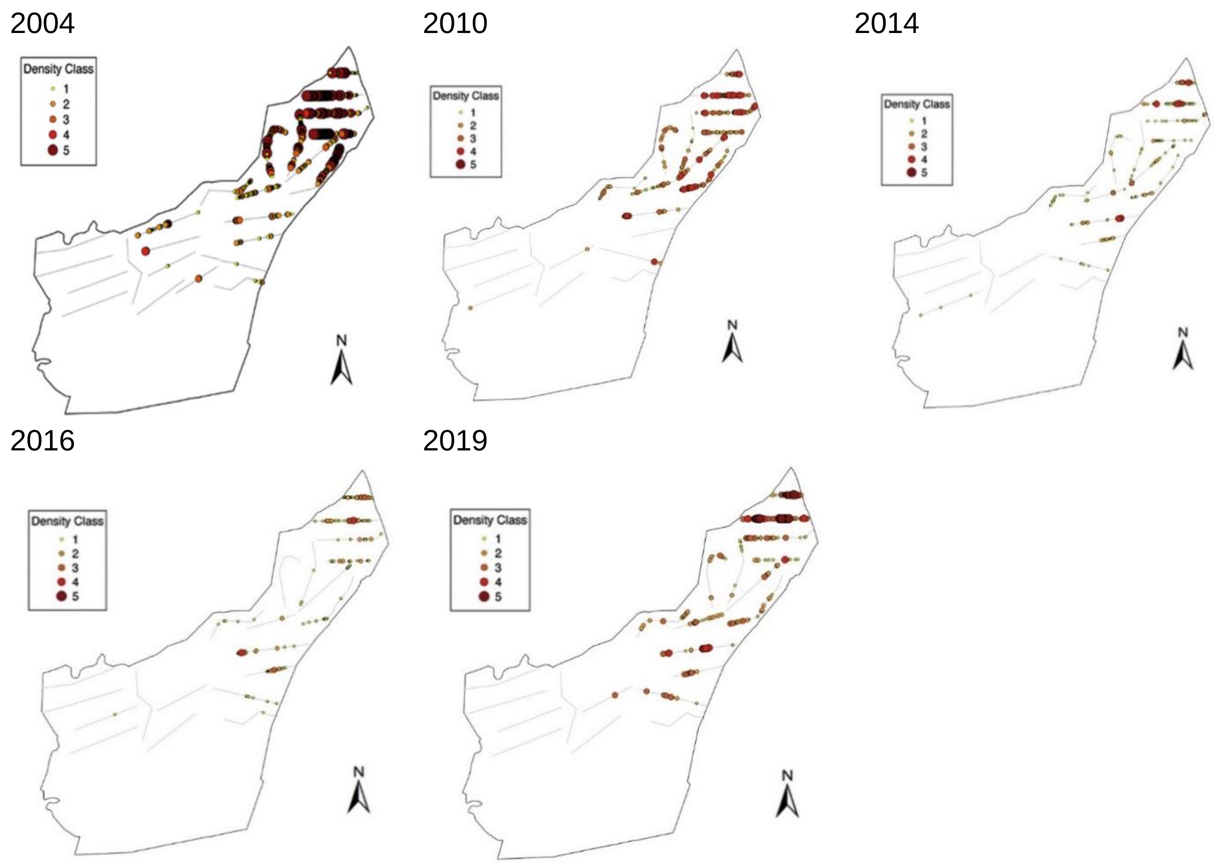
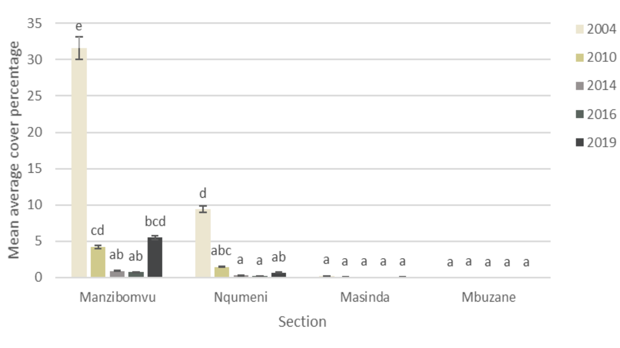


Figure 5 The distribution and density of C. odorata from 2004-2019 are displayed over 5 maps. The legend is displaying 5 categories of density, according to the plant cover indication scale explained in the Method chapter.

Figure 8 shows that the density of *C. odorata* of 2004 are not even nearly matched in succeeding years. 2004 was the height of the invasion of *C. odorata* in HiP. However, it does show that the density is increasing again in 2019, especially in the northern sections of the park. Figure 8 also indicates that the *C. odorata* has almost dissapearedin 2014 and 2016, but it came back in 2019. Figure 9 shows that the relation between *C. odorata* levels and the annual rainfall levels.



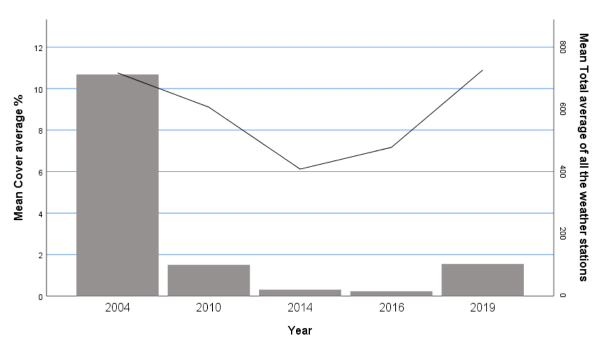


Figure 8 the mean cover average percentage of C. odorata for each section per year.

Figure 9 the cover average percentage of C. odorata for each year in relation to the annual rainfall.

Figure 10 gives an indication about the distribution of *C. odorata*, not so much about the density of *C. odorata*. Where figure 9 shows that *C. odorata* is almost gone, in figure 10 it can be seen it is still widely spread, not in high denisties, but still there. It can be seen that *C. odorata* has decreased over the years, however it has never been fully eridacted and as of 2019 it is increasing again. Figure 11 indicates a relation between the *C. odorata* fluctuations and the annual rainfall.

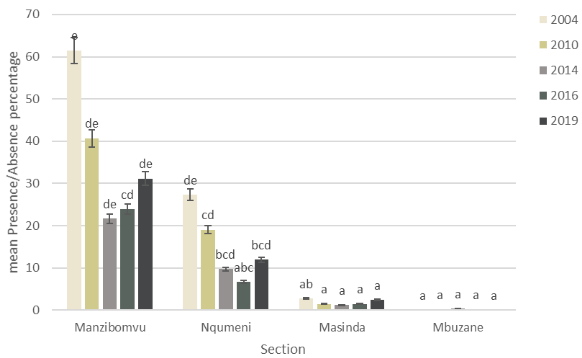


Figure 10 the presence/absence for each section per year is displayed.

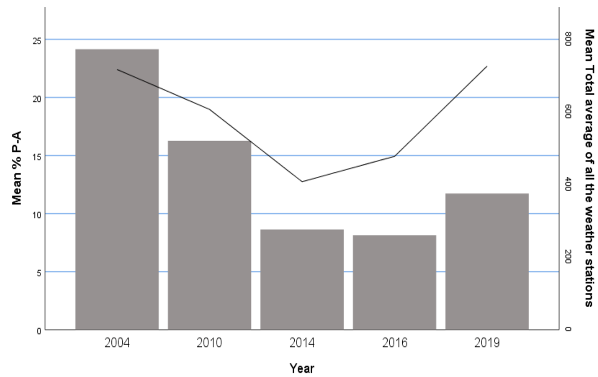


Figure 11 the presence/absence for each year is displayed in relation to the annual rainfall.

In table 3 it can be seen that both tests indicate significance for all the fixed factors (p=<0.05). This means that the *C. odorata* presence significantly differed across the different years, especially in 2004, in Manzibomvu and Nqumeni. The fixed factors Year and Section have a P value smaller than 0.0001.

		P/A		*Average cover percenatge*	
	Df	F	P	F	P
Year	4	**19.10**	**<0.0001**	**18.70**	**<0.0001**
Section	3	**80.50**	**<0.0001**	**41.70**	**<0.0001**
*Year*Section*	12	**3.96**	**<0.0001**	**6.40**	**<0.0001**
Error	85				

Table 3 the results of the univariate ANOVA models for the presence/absence and the average cover percentage.

The effect of spatiotemporal water availability on the distriution and density of 5 priority invasive species

Below the distribution and density of the 5 priority invasive species is elaborated upon, *O. aurantiaca* is not included in this result section because that species is not observed in the park. Figure 12 shows a strong increase of invasives in Mazibomvu in 2019, compares to preceeding years. The average cover percentage shows that the total number of invasives has decreased in 2016 compared to 2014.The invasives seem te relate with the annual rainfall patterns for 2014 and 2019(fig. 13). The cover decreases for 2016, it however increases abundantly in 2019. The mean annual rainfall does not decrease at all.

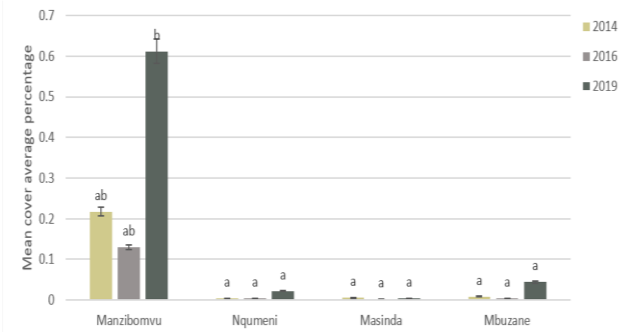


Figure 12 the cover average percentage of 4 invasive species for each year is displayed in relation to the annual rainfall.

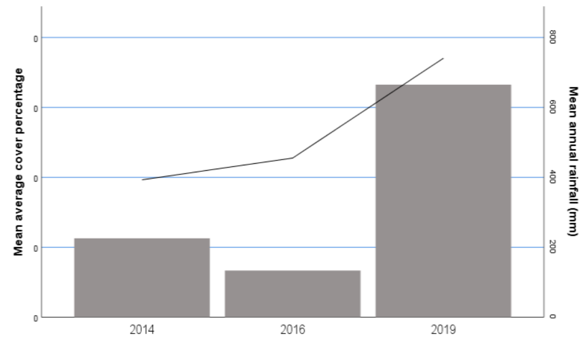


Figure 13 The cover average percentage for 4 invasive species for each section per year is displayed.

Manzibomvu is the most abundant in the presence/absence of invasive species in the years 2014, 2016 and 2019, which increases gradually over the years. The same trend is seen in the Nqumeni and Masinda section. Mbuzane shows a slight decrease in invasives in 2016, however it increases compared to 2014 again in 2019 (fig. 14).

In figure 15 it can be seen that the mean annual rainfall line seems to relate with the mean presence/absence levels of the invasive species.

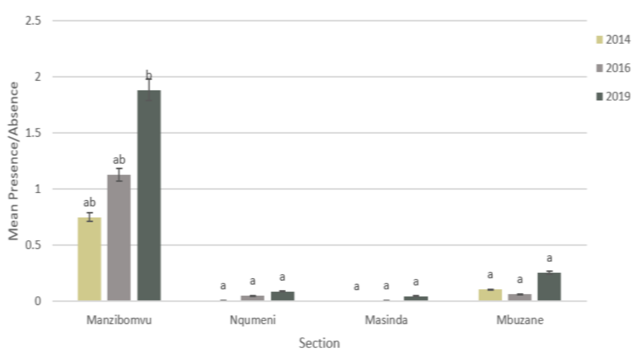


Figure 14 The presence/absence of 4 invasive species for the years 2014, 2016 and 2019 in each section of HiP

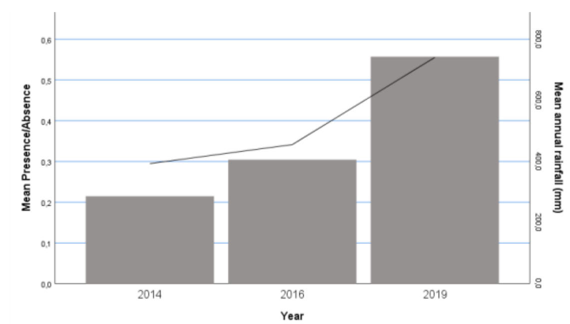


Figure 15 The presence/absence of 4 invasive species for the years 2014, 2016, and 2019, in relation to the annual rainfall

Table 4 below describes the results of the general linear models for the presence/absence and the average cover percentage. Both of the tests indicate a significance (P=<0.05) for the fixed factors; year, section, species and section*species. Only the average cover percentage shows a significance for the fixed factor year*section.

		P/A		Average cover %	
	Df	*F*	*P*	*F*	*P*
Year	2	**2,70**	**0,069**	**4.711**	**0,010**
Section	3	**41,8**	**<0,0001**	**21.646**	**<0.0001**
Species	3	**25,4**	**<0,0001**	**9.656**	**<0,0001**
*Year*Section*	6	0,72	0,637	**2,787**	**0,013**
*Year*Species*	6	0,25	0,980	0.316	0,928
*Section*Species*	9	**13,8**	**<0,0001**	**12.241**	**<0,0001**
*Year*Section*Species*	18	0,23	1	0,760	0,745
Error	204				

*Table 4 general linear model for the dependent variables presence/absence and the average cover percentage for the fixed factors year, section, species and section*species*

L. camara

In figure 16 below its displayed how *L. camara* has increased from 2014-2019. This increase is initially happening in the northern sections, however in 2019 *L. camara* is also observed in the most southern sections. On transect 3 the species is most abundant.

2014 *2016* *2019*

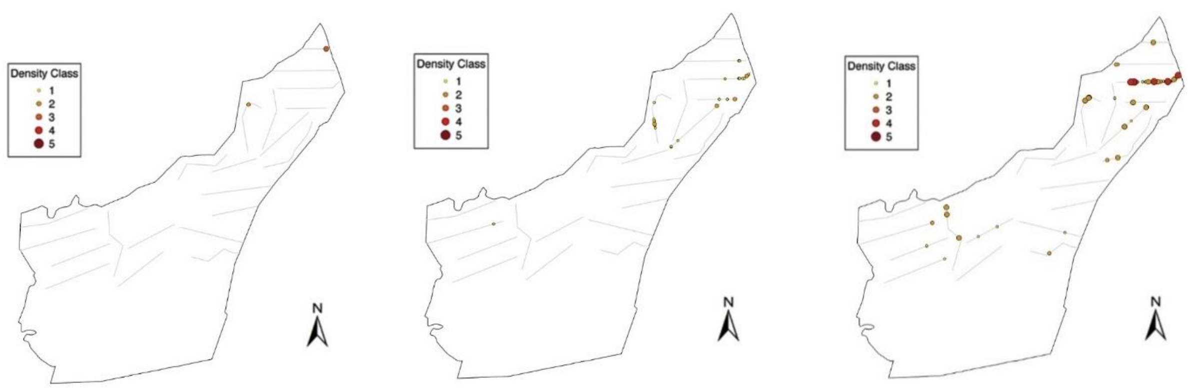


Figure 16 The distribution and density of L. camara in HiP in 2014, 2016 and 2019

L. camara is mostly active in the northern section Manzibomvu, especially in 2019. It has significantly increased in density and in distribution in that section. In 2019, it also starts appearing in Nqumeni, the more arid section.

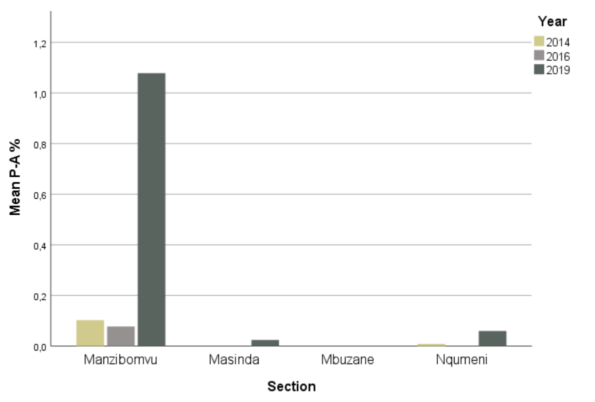


Figure 17 The presence/absence of L. camara per section in the years 2014, 2016 and 2019

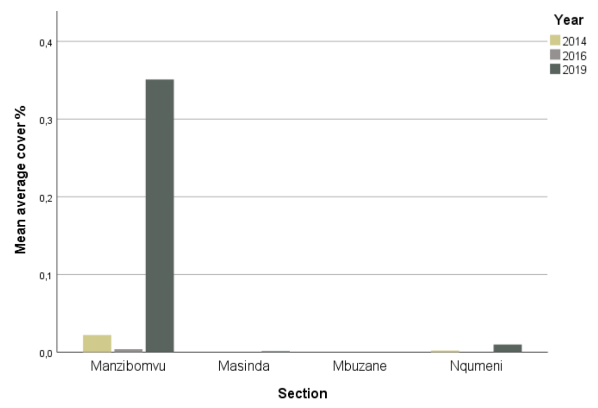


Figure 18 The Average cover percentage of L. camara per section in the years 2014, 2016 and 2019

P. hysterophorus

P. hysterophorus shows an increase in distribution and in density going from 2014 to 2019 (fig. 19). In 2016 an increase of the invasive is observed at the most eastern part of transect 3, where as in 2019 transect 3 is once again the most invaded transect. The species seems to be appearing in the southern sections as well, in wetter years.

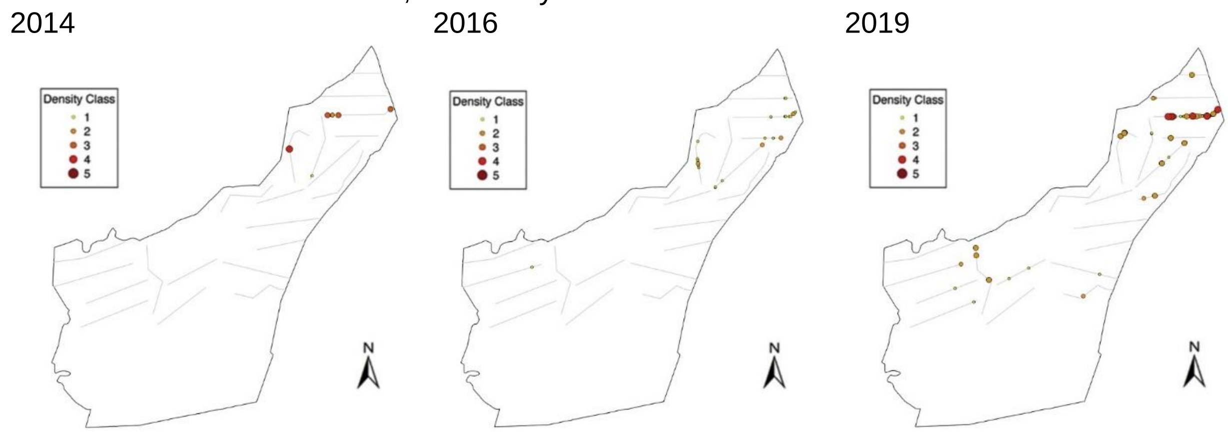


Figure 19 The distribution and density of P. hysterophorus in HiP in 2014, 2016 and 2019

An overall increase in density and distribution is seen in figure 20 and 21. The largest increase is seen in the northern section, just like *L. camara*, but this species also shows a clear increase and appearance in other sections. It is appearing in Masinda and in Mbuzane, and increasing in Nqumeni

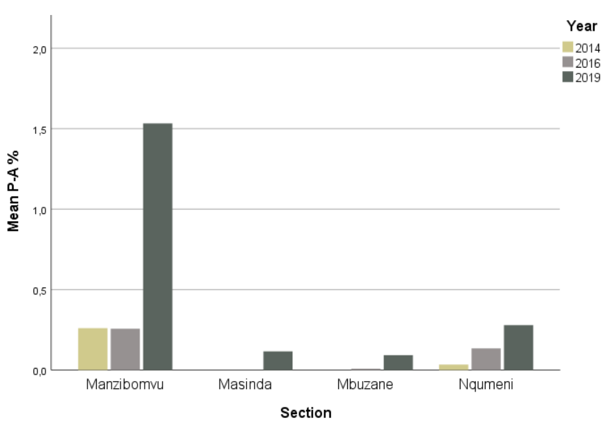


Figure 20 The presence/absence of P. hysterophorus per section in the years 2014, 2016 and 2019

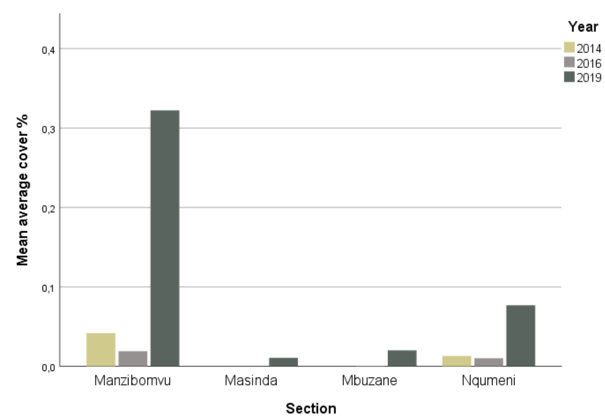


Figure 21 The presence/absence of P. hysterophorus per section in the years 2014, 2016 and 2019

T. minuta

In 2014 *T. minuta* seems to be the most widely spread among the sections (fig. 22). In 2019 the density however is more concentrated the northern sections, and has moved away from the southern ones. Transect 3 seems to be the most densely invaded transect.

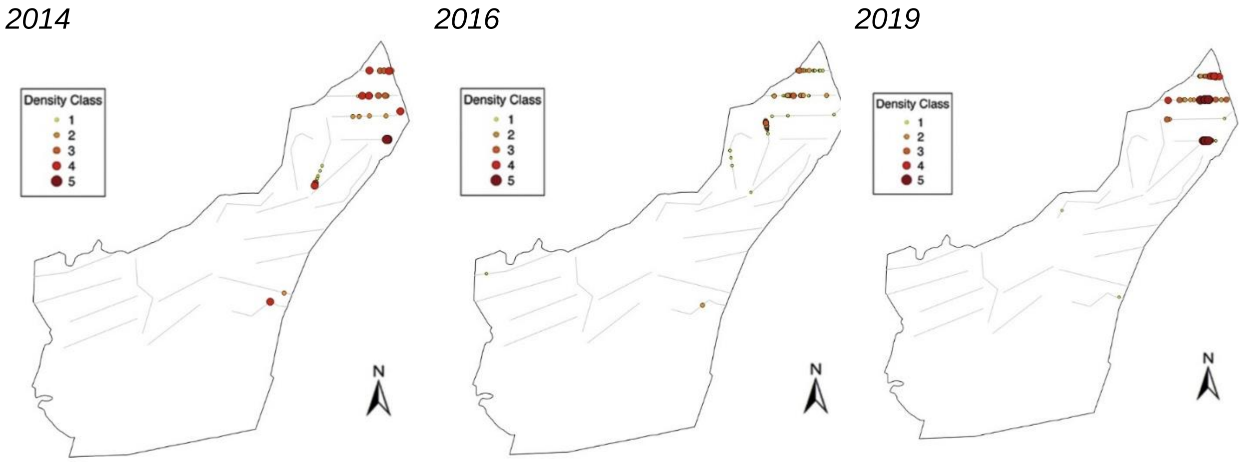


Figure 22 The distribution and density of T. minuta in HiP in 2014, 2016 and 2019

The distribution has only increased from 2014 to 2019, the density has first decreased in 2016 and then increased again in 2019.

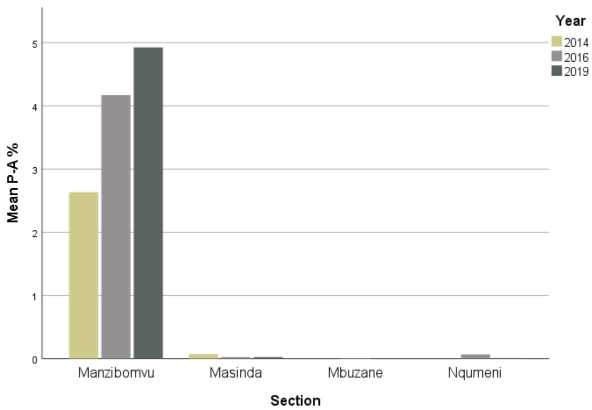


Figure 23 The presence/absence of T. minuta per section in the years 2014, 2016 and 2019

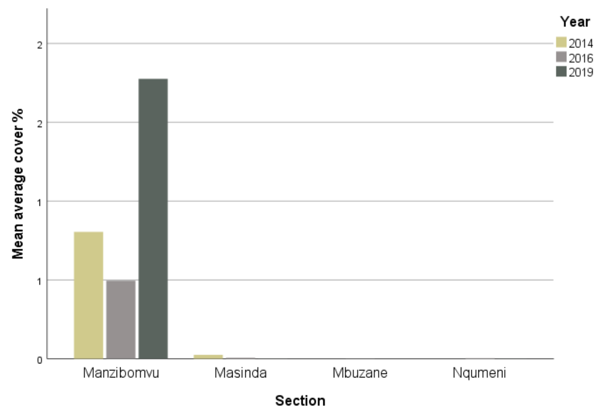


Figure 24 The presence/absence of T. minuta per section in the years 2014, 2016 and 2019

O. ficus-indica

O. ficus-indica is mostly located in the southern section of the park. In 2019 it starts to make its way to Masinda, the transect east to Mbuzane. The total number of *Opuntia* has increased as well.

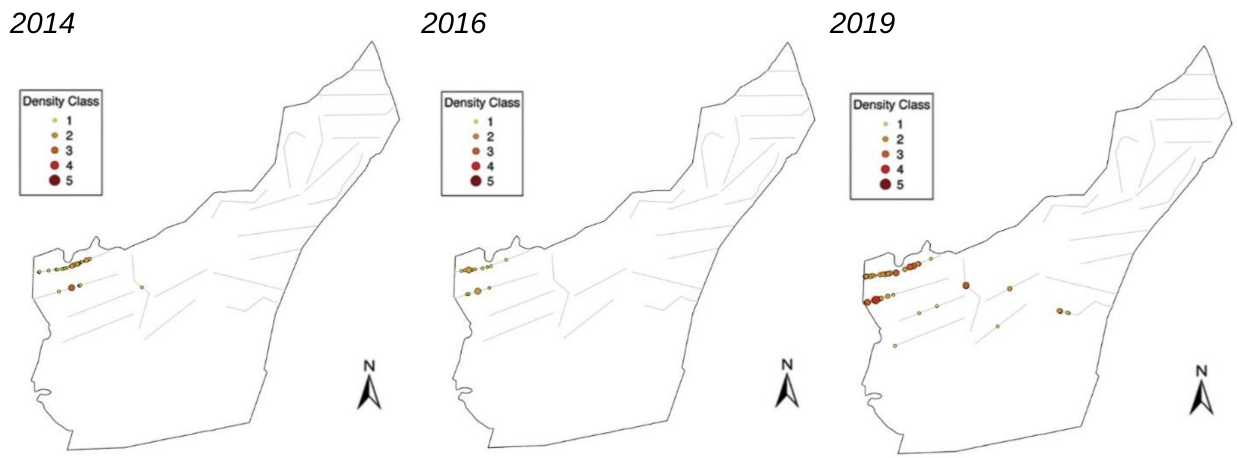


Figure 6 The distribution and density of Opuntia in HiP in 2014, 2016 and 2019

The species is most abundant in Mbuzane, especially in 2019. The species starts appearing in 2019 in Masinda.

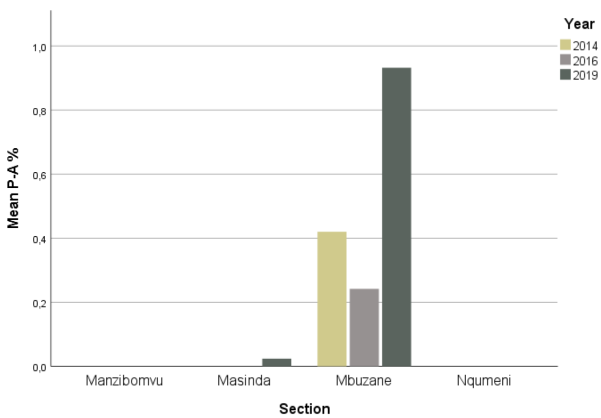


Figure 26 The presence/absence of O. ficus-indica per section in the years 2014, 2016 and 2019

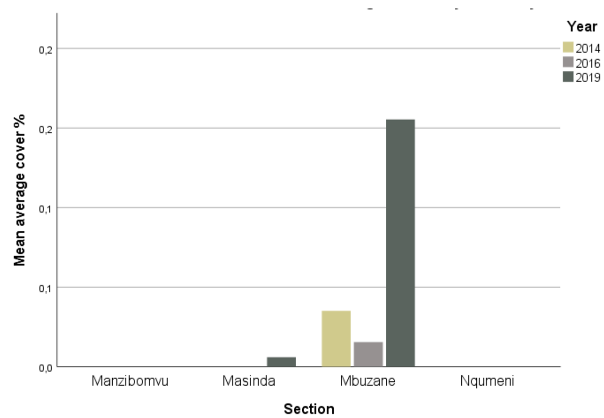


Figure 27 The presence/absence of O. ficus-indica per section in the years 2014, 2016 and 2019

The most abundant of the priority invasive species is *T. minuta*, it is most abundant in the Manzibomvu section (fig 28 and 29). In Mbuzane the most abundant species is the *Opuntia*.

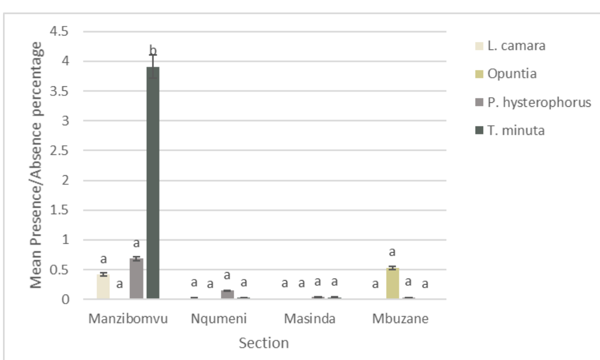


Figure 28 The presence/absence of all species per section in the years 2014, 2016 and 2019

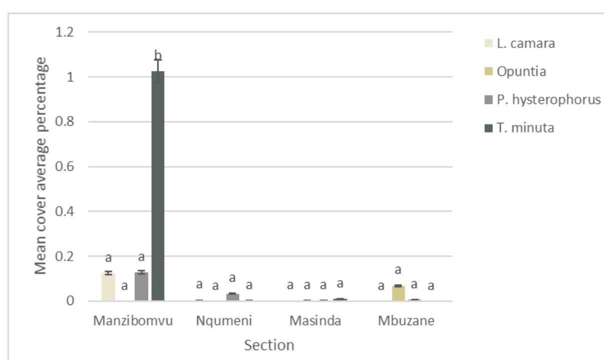


Figure 29 The presence/absence of all species per section in the years 2014, 2016 and 2019

Table 5 shows the results of a General Linear Model for each of the priority invasive species of HiP. The Presence/Absence and the average cover was used as a dependent variable. The fixed factors were the Year and the Section, as a proxy for temporal and spatial variations in water availability. *T. minuta, P. hysterophorus* and *O. ficus-indica* show a significance (p=<0.05) for the spatial aspect as both the presence/absence and average cover as a dependent variable. *L. camara* only shows significance for the spatial aspect, with the presence/absence as a dependent variable. *P. hysterophorus* is the only species that shows significance for the temporal aspect with presence/absence as a dependent variable.

		P/A		Average cover	
T. minuta	Df	F	P	F	P
Year	2	0.108	0.898	1.052	0.357
Section	3	**26.290**	**<0.0001**	**19.614**	**<0.0001**
Year*Section	6	0.150	0.988	1.199	0.322
Error	51				
P. hysterophorus	Df	F	P	F	P
Year	2	**3.384**	**0.038**	4.142	0.22
Section	3	**4.792**	**0.005**	**3.365**	**0.026**
Year*Section	6	0.851	0.537	1.677	0.146
Error	51				
L. Camara	Df	F	P	F	P
Year	2	1.422	0.251	1.397	0.257
Section	3	**2.491**	**0.071**	1.815	0.156
Year*Section	6	0.915	0.492	1.313	0.268
Error	51				
O. ficus-indica	Df	F	P	F	P
Year	2	0.484	0.619	1.204	0.308
Section	3	**5.534**	**0.002**	**3.601**	**0.019**
Year*Section	6	0.481	0.819	1.273	0.286
Error	51				

Table 5 A general linear model with the dependent variables Presence/Absence and average cover percentage, and the fixed factors Year and Section for each of the priority invasive species

The effect of spatiotemporal water availability on the distriution and density the CRS groups

As can be seen in figure 30 the competitor species seem to florish in the northern sections of the park, and move away from the most southern ones. The group seems to have increased in 2019. The ruderals have start moving to the southern sections opposed to the competitors, it is still mostly located in the northern sections. The stress tolerators are moving located in the most southern sections and also start appearing in the more eastern section.

2014 2016 2019

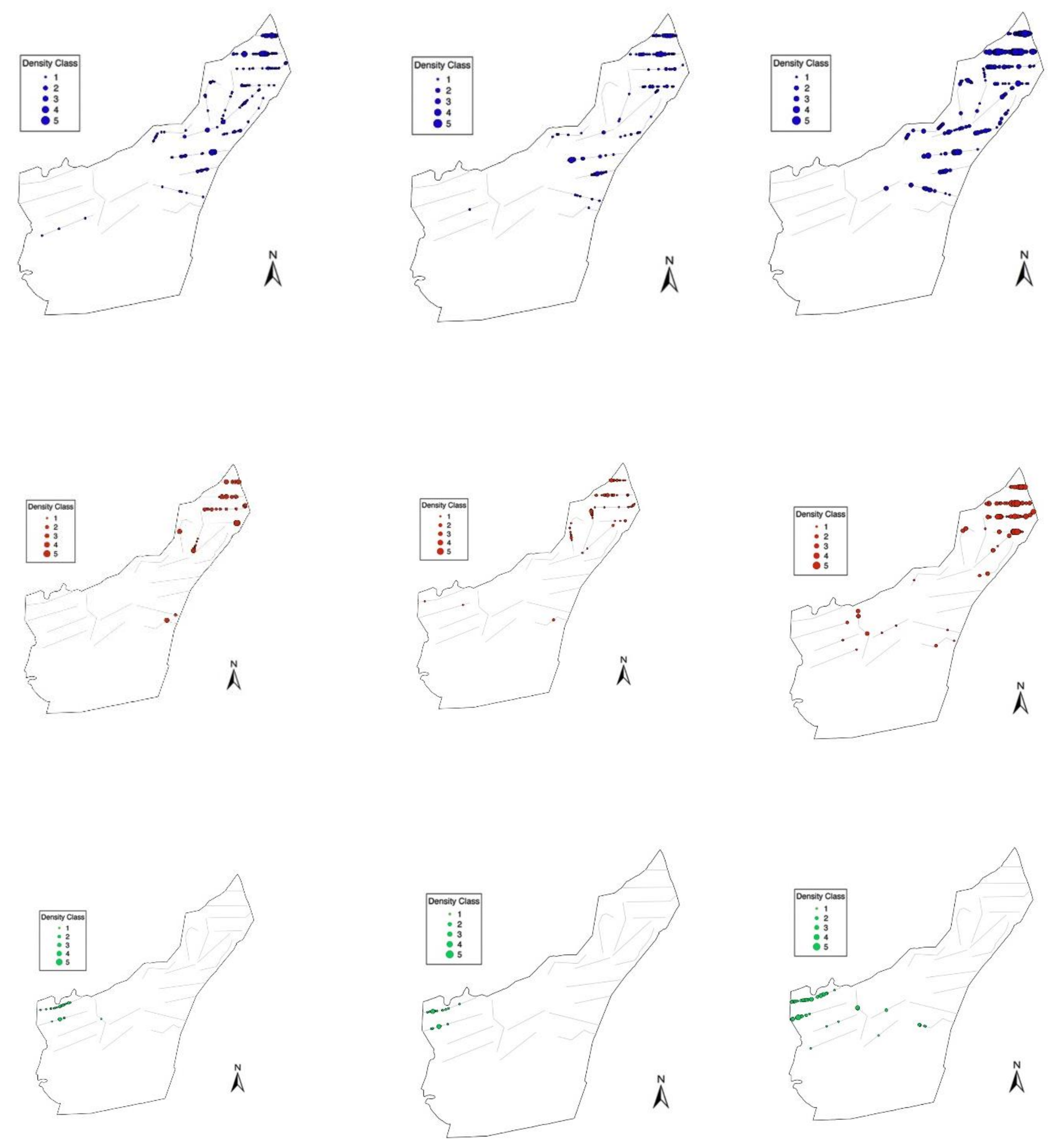


Figure 30 the distribution and density of the all the invasive species in HiP for 2014, 2016 and 2019 categorized as competitor (blue), Ruderal (red), or stress tolerator (green)

Figure 31 and 32 shows the spatial distriubtion and density of the CRS groups. It indicates that the ruderals appear in the same sections as the competitors, but are not as abundant. The stresstolerant species only appear in Mbuzane, the most southern and arid sections of the park. The figure shows that the competitors

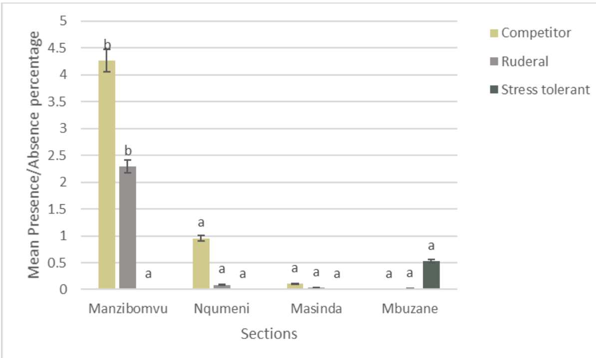


Figure 31 The spatial distribution of the CRS groups in HiP.

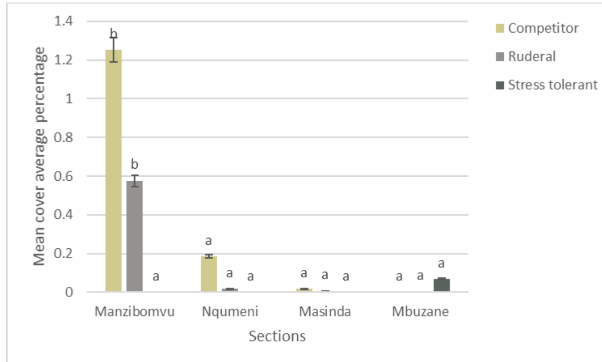


Figure 32 The spatial density of CRS groups in HiP

Table 6 shows that the P/A and average cover percentage are signigicant with the group and with the section (p=<0.05). The dependent variables shows no significance with the temporal factor year, it does however with the spatial factor.

		P/A		Average cover %	
	df	F	P	F	P
Group	2	**6.82**	**0.001**	**3.867**	**0.022**
Section	3	**14.6**	**<0.0001**	**10.943**	**<0.0001**
Year	2	1.30	0.274	**3.298**	**0.038**
Group*Section	6	**6.84**	**<0.0001**	**3.223**	**0.004**
Group*Year	4	0.105	0.981	0.6	0.663
Section*Year	6	0.244	0.961	1.33	0.244
Group*Section*Year	12	0.22	0.997	0.52	0.901
Error	279				

Table 6 a General Linear Model for the CRS groups with the Presence/Absence and Average cover percentage as dependent variables and the group, year and section as fixed factors.

Discussion

Water availability

So what we can tell from the results regarding the spatial and temporal vairaitions in water availability is that there seems to be a period of low water availability in 2014 and 2015 in HiP. Also we can see that the northern sections deal with significantly more rainfall than the southern sections.

C. odorata

As to be expected and in line with the hypothesis described in the first chapter, the distriubtion and density of *C. odorata* has reduced as water availability levels decreased. When water availability levels rise again so does the amount of *C. odorata*. In the General Linear Models we can see a significance between the spatial and temporal water availability. A significance between *C. odorata* distribution and density and both spatial and temporal water availability.

In 2004, the height of the *C. odorata* invasion in HiP, the WfW started removing the invasive species in the park. This also explains the decrease in *C. odorata* that is shown in the maps for 2010, 2014, and 2016. In addition, in 2016 the WfW stopped its removal campaign due to an unfortunate incident in the park. Now, this explains the increase of *C. odorata* starting in 2016 as well. A combination of variations in water availability and the practices of the removal programme seem to be responsible for the levels of *C. odorata* in the park.

When we look at the cover average percentage of *C. odorata* (fig. 8 and 9) it seems like that in 2014 and 2016 *C. odorata* is almost eridicated in HiP. However, when we look at the presence/absence (fig. 10 and 11) we can see that dispite the *C. odorata* density levels were low, it was still widely spread in 2014 and 2016. Which in combination with the stop of the removal program and the increasing water availability levels might explain the strong return of *C. odorata* in 2019. Regardless of its cause the distribution and density of *C. odorata* in HiP are increasing again, and this can have severe consequences for the ecological wellbeing of the park.

Priority species & CRS groups

L. camara shows no significant relation with variations in spatial or temporal availability of water. All but *P. hysterophorus* show a significant temporal relation. It makes sense that the other species do not show this significance, because for these analysis we are missing the base year of 2004 and data for the years before the drought, making it hard to run an analysis for temporal relations. *T. minuta, P. hysterophorus and opuntia* show a significance with spatial water availability.

An interesting trend we can spot when we look at the maps of *L. camara* and *P. hysterophorus*, is that these invasive species are abundant on transect 3, notably in the eastern part of that transect. Now there could be multiple explanations for that, but one of them could be regarding the entrance gate that is located at the eastern end of transect 3. Memorial gate is located there, and this is the gate where both tourist and employees enter the park. This could indicate that people are actually bringing seedlings from these invasive species in, knowingly or unknowingly.

In the general linear models no significance is found for the response on variations in temporal water availability for any of the CRS groups. We did however find a significance for the groups and the variations in spatial water availability.

The results seem to concide with the hypothesis of the competitors. They seem to do well in the northern sections, and are decreasing during the drought, and increasing right after the drought. They are also spreading into the more southern sections in 2019, this can be explained by the *L. camara*, that is more resilient during drought events. *L. camara* is increasing in the northern sections and in 2019 it appears in Masinda and Nqumeni, indicating it does well in dryer areas. In both the temporal and spatial aspect the ruderals were found mostly in the northern section Manzibomvu. In 2019 they do also spread to more southern sections, but that is *P. hysterophorus*, not *T. minuta.* The stress tolerant species are found in the southern sections, in 2019 it is moving more eastward, to the Masinda section. This regards only *O. ficus-indica*, *O aurantiaca* has not been observerd on any of the transect on the parks. That does not mean it is not present. The species could be present on the transects that were not walked, or in Makhamisa, the wilderness section.

Limitations

While doing this research there have been a couple of restrictions that should be taken into account. Some of the transects could not be walked due to high river levels, crossing them would be too dangerous because of bad visibility. This regarded transect 13, 14 and 17.

The collection period was different then previous years. In those years the data was collected in the winter months, while the data of 2019 was collected in the summer months. The density and distribution of plant species can differ quite a bit in these different periods. As there are large variations in water availability and in temperature between these periods.

Also, observer bias has to be considered when looking at the results. In every data collection year the collection was done by a different observer. A different observer might estimate a plot in a different way.

This study did not include the impact of herbivores, variations in nutritient supply or temperature in account, when looking at the distribution and density of the 6 alien invasive plant species. This is due to time restrictions.

Conclusion

The main findings from this study show that all the observerd alien invasive species have significantly increased in 2019. Also, the abundane of invasive species are found in Manzibomvu, the section with the most rainfall. These findings seem to agree with the trends in spatial and temporal water availability. They also seem to relate to the practises of the WfW programme, notably the hold up of it in 2016, especially for *C. odorata*. *C. odorata* has increased the most in 2019 and is still the most abundant invasive species in HiP. This is worrysome, especially when we consider that the invasive species was almost eridicated in 2014, and despite that has made a significant comeback in 2019. This is an important message for the management of HiP, the removal program had an significant impact, but these tenacious invasive species are resilient and are coming back. Based on these findings it is recommended that the park starts the removal programme for *C. odorata* once again, and this time continues until it the invasives are fully eredicated. The monitoring of the distribution and density of the alien invasive species should continue, also in Makhamisa, the wilderness section. In order to study the response of alien invasive species on water availability or on extreme climatic events, more inclusive studies are recommendend. Studies in which the ground water and river water availablity levels are included and studies in which the nutrient flows and variations in temperature are included.

In addition, an important finding is the abundance of *L. camara* and *P. hysterophorus* on the eastern end of transect 3. As mentioned before memorial gate is located there, and this might indicate that the species are entering the park here. More research regarding this occurrence is recommended. Measures and policies that aim at preventing further penetration of any alien invasive plant species in HiP are recommended.

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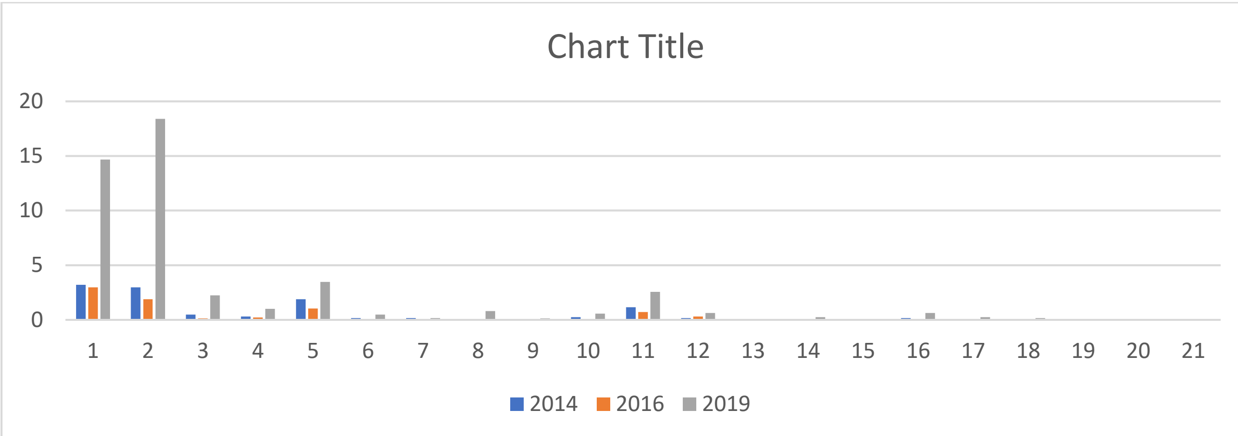
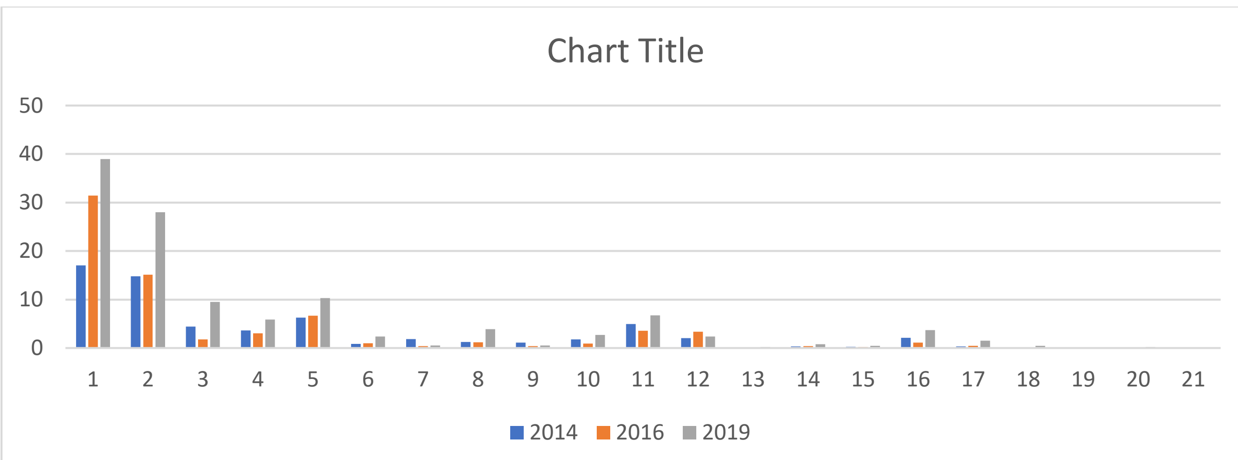
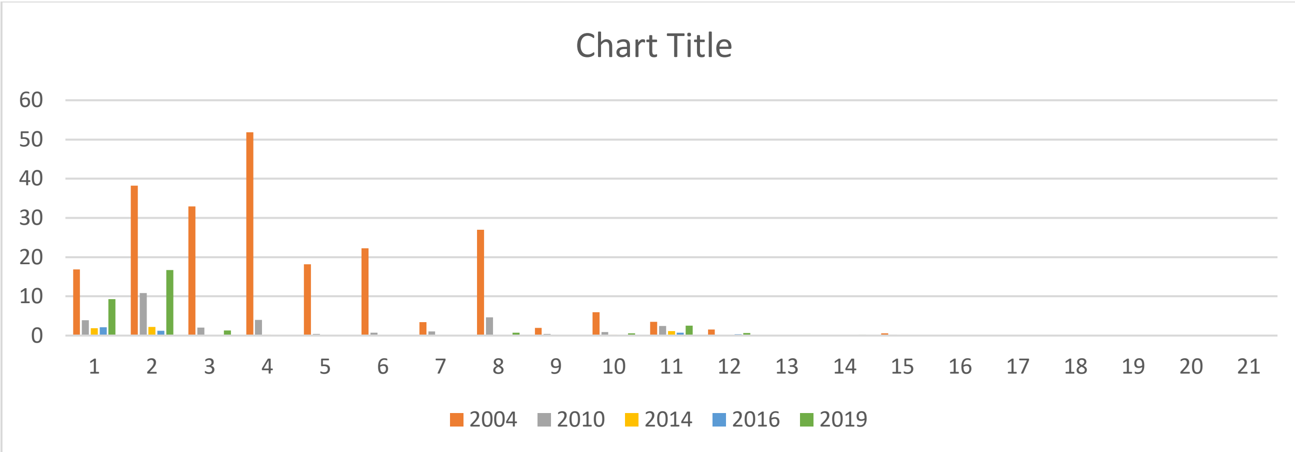
Appendix I: Results Density and distribution of all invasive species in HiP

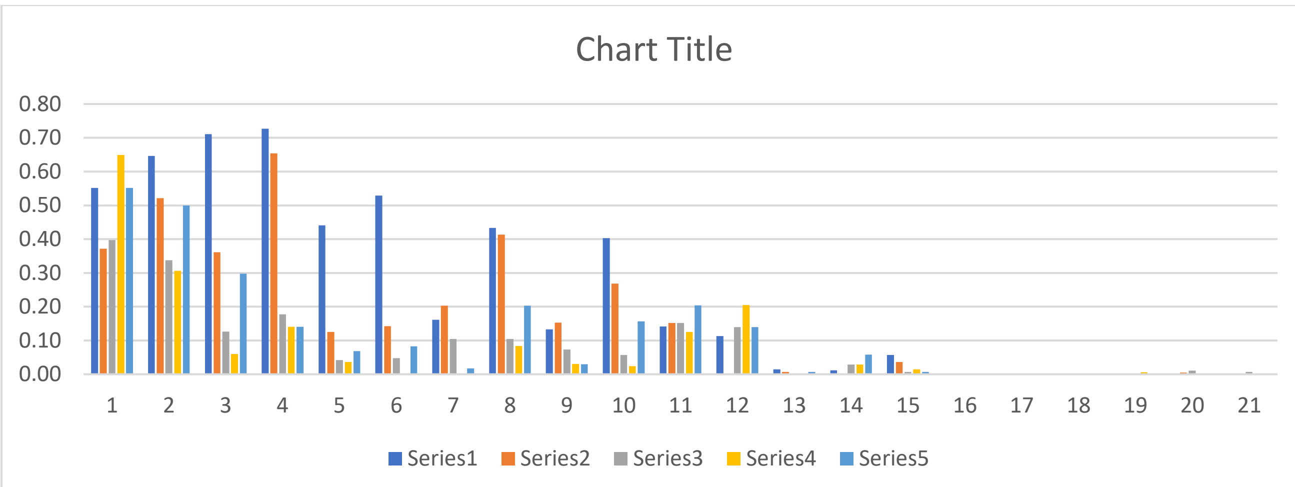
Results density & distribution all species

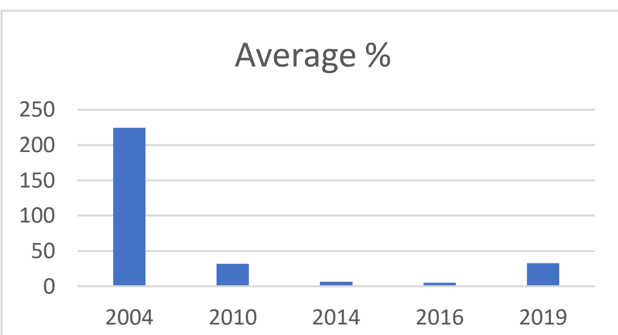


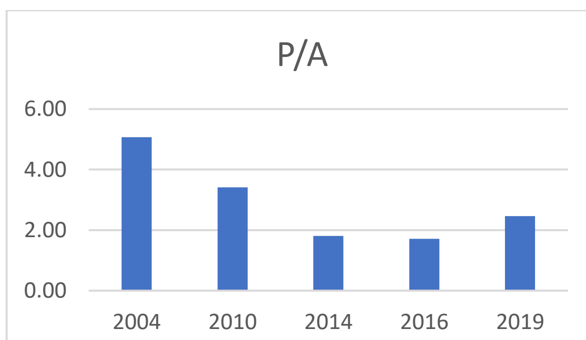


Appendix II: Results Density and distribution *C. odorata*



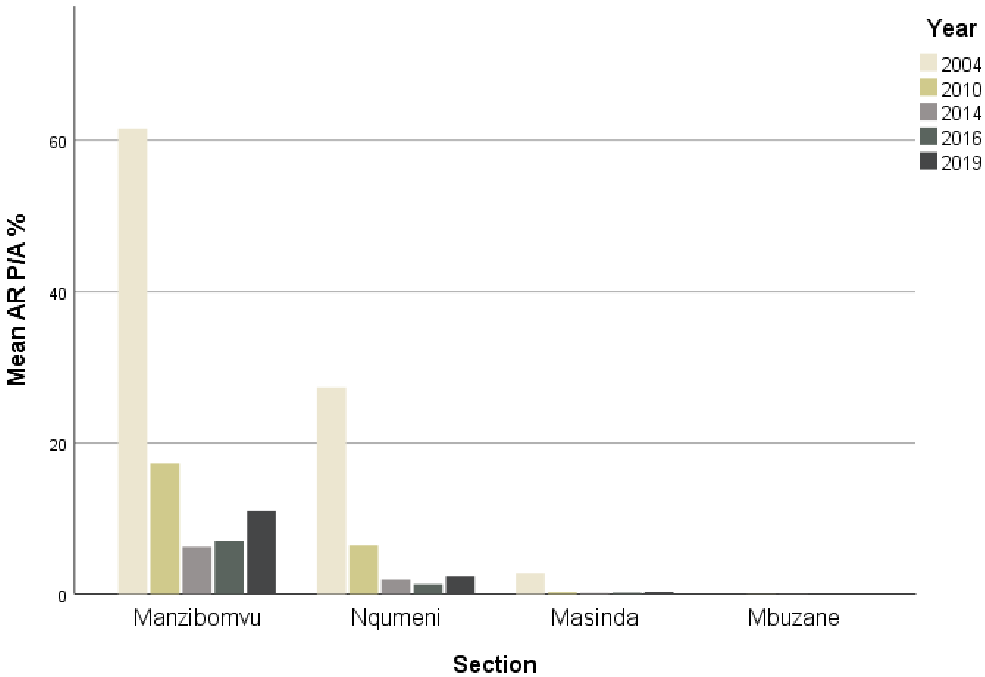


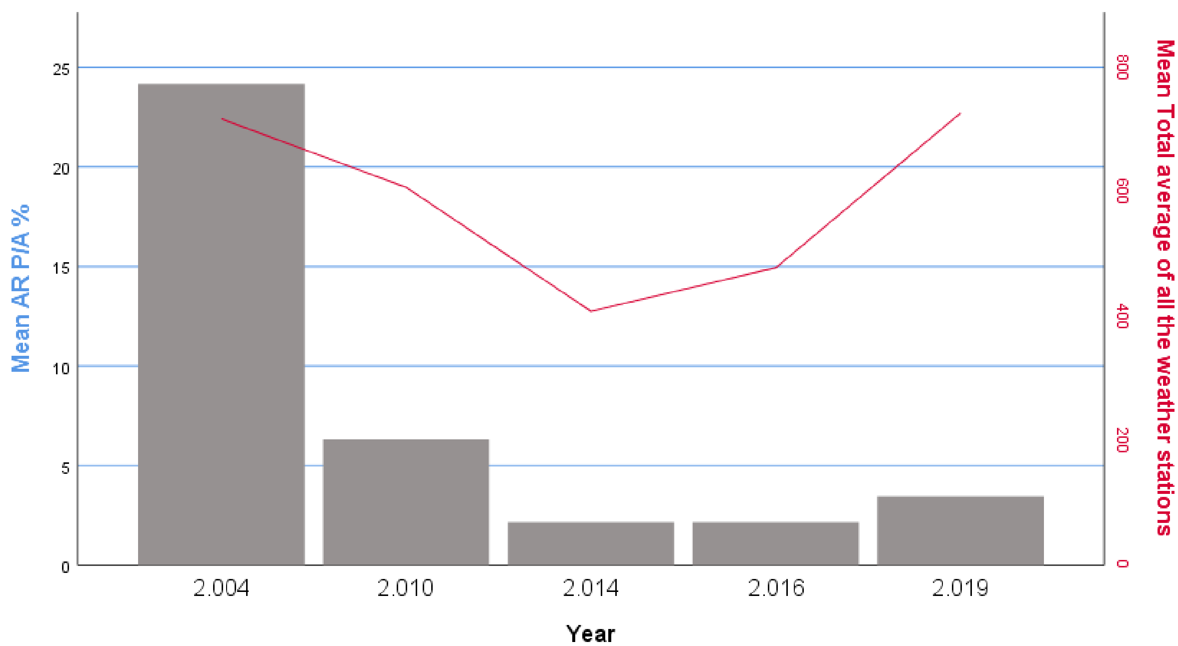




Appendix III: Actual Resolution *C. odorata*

In figure **X** the actual resolution presence/absence for each section per year is displayed.





Appendix IV: Distribution and density 4 priority species

P. hysterophorus

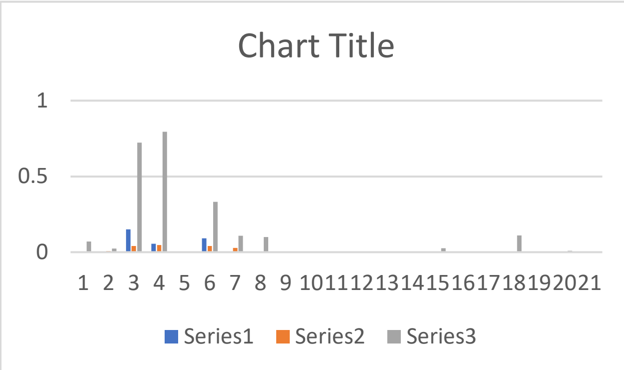


Figura 1 Cover average percentage P. hysterophorus

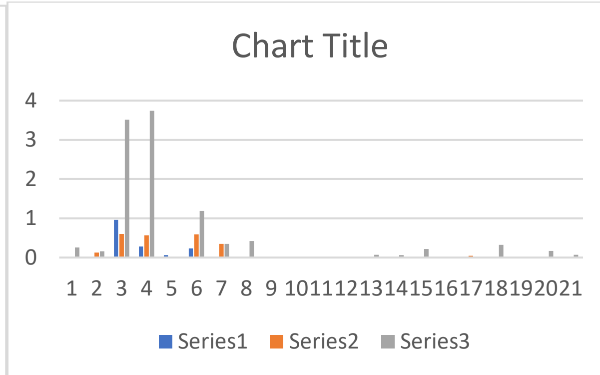


Figura 2 Presence/Absence P. hysterophorus

L. camara

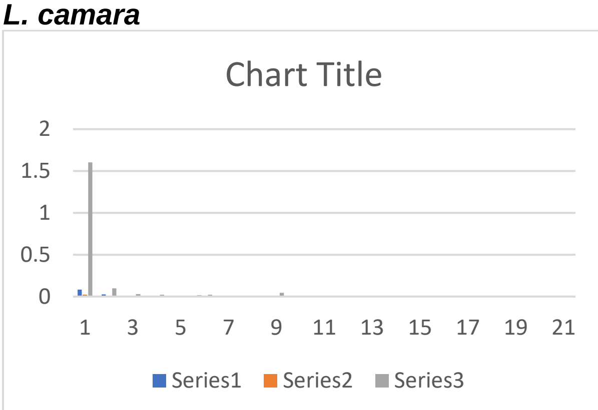


Figura 3 Cover average percentage L. Camara

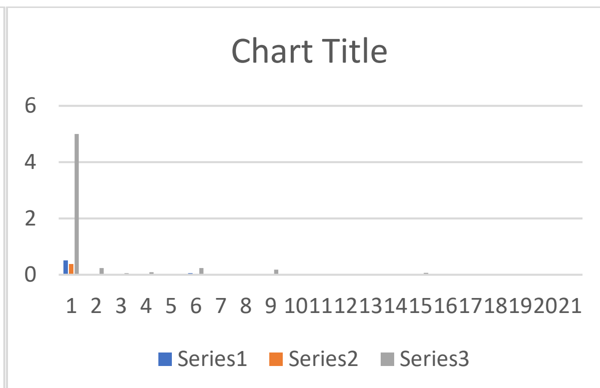


Figura 4 Presence/Absence L. camara

T. minuta

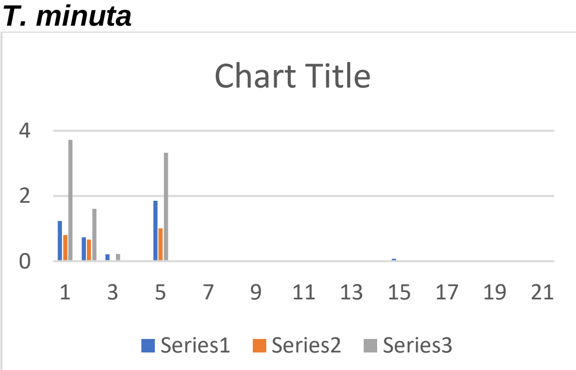


Figura 5 Cover average percentage T. minuta

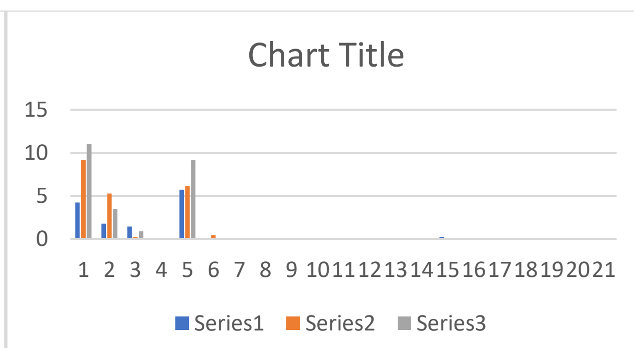
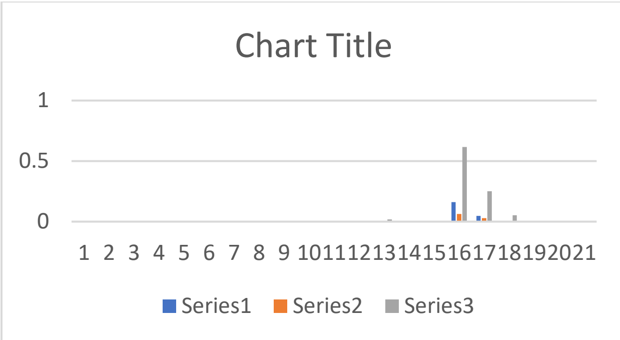


Figura 6 Presence/Absence T. minuta

Opuntia



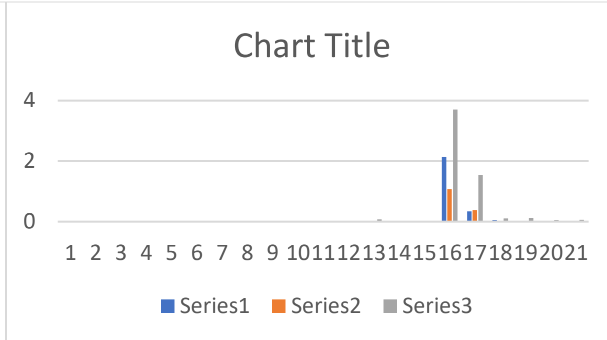
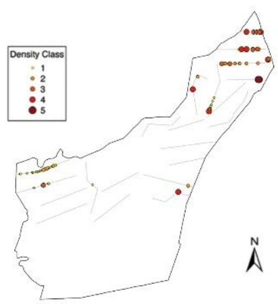


Figura 7 Cover average percentage Opuntia

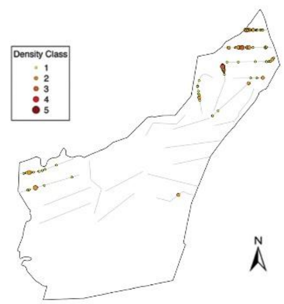
Figura 8 Presence/Absence Opuntia

Appendix V: Map all species in HiP

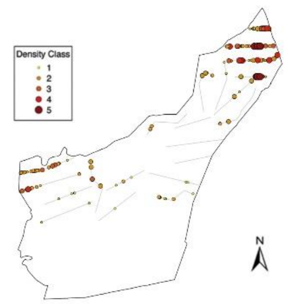
2014



2016



2019



Appendix VI: Q-Q/Shapiro test

LOG(Y+1)