Prosopis invasions in South Africa: Population structures and impacts on native tree population stability

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ABSTRACT

Several *Prosopis* taxa are widespread invaders that have negative impacts on biodiversity and human livelihoods globally. Better knowledge of the impacts and ecology of invasive *Prosopis* species is required to support and inform management interventions. *Prosopis* was introduced to South Africa and has become the second most widespread invasive alien plant taxon in the country. We compare population structures of invasive *Prosopis* populations in different part of South Africa, and quantify the effects of *Prosopis* invasions on native tree populations using size-class distribution (SCD) curves. Kolmogorov–Smirnov tests, regressions, quotients, and Permutation Indices were used to compare size-class distributions and assess population stability. *Prosopis* population structures differed across South Africa. Those along perennial rivers and areas in the Succulent Karoo biome had fewer juvenile plants. *Prosopis* in South Africa also has higher recruitment (% juvenile plants) than in other areas like Australia. *Prosopis* invasions are having a negative effect on the stability of native tree populations in South Africa, and are linked to increased mortality of native trees. Improved management of *Prosopis* is needed.

1. Introduction

Invasive alien species are a key driver of biodiversity loss and ecosystem function disruption globally (Wilcove et al., 1998). They are a major cause of mammal, bird and fish species extinctions, and also threaten plant diversity in many regions (Gaertner et al., 2009). Biological invasions lead to the suppression of native plants by competing for limited resources (Richardson et al., 1989). The understanding of the impacts of invasive alien species at a community levels is, however, rather limited and further research is needed especially over large spatial and temporal scales (Tickner et al., 2001). Taxa in the genus *Prosopis* (mesquite) have been introduced and become naturalized or invasive in many of the world's arid and semi-arid areas (Rejmánek and Richardson, 2013). *Prosopis* has been highlighted as a serious invasive alien taxon globally and poses threats to biodiversity and human activities, but further research on impacts and ecology is needed (Shackleton et al., 2014). These *Prosopis* invasions have been shown to have a negative impact on native plant, bird and turtle populations in many countries (Belton, 2008; Kaur et al., 2012; Muturi et al., 2013).

Prosopis taxa were introduced to South Africa in the late 19th century and were actively distributed and planted in the semi-arid and arid parts of the country, especially in the 1960s and 1970s (Zimmermann, 1991). Several species and their hybrids are now major invaders across large parts of the arid interior of South Africa. Common species include *Prosopis chilensis*, *Prosopis glandulosa* and *Prosopis velutina*, and their freely inter-breeding hybrids (Zimmermann, 1991; Poynton, 2009; Mazibuko, 2012). There is also evidence that *Prosopis alba*, *Prosopis juliflora*, *Prosopis laevigata*, *Prosopis pallida*, *Prosopis pubescens* are also present but not as common (Mazibuko, 2012). *Prosopis* invasions now cover at least 1.8 million ha of South Africa (Versfeld et al., 1988) and are expanding at around 8% per annum (Van den Berg, 2010). Invasions have had severe negative impacts on ecosystem services such as water and grazing supply (Ndhlovu et al., 2011; Dzikiti et al., 2013) and are adversely affecting native plant, bird and insect species richness and diversity (Steenkamp and Chown, 1996; Dean et al., 2002; Ndhlovu et al., 2011; Shachtschneider and February, 2013).

An integrated approach to managing *Prosopis* is being implemented in South Africa to reduce the impacts of invasions. This includes biological control using seed-feeding beetles (*Algarobius prosopis*, *Algarobius bottimeri* and *Neltumius arizonensis*) (Zimmermann, 1991) and mechanical and chemical control

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implemented mainly by the government-run Working for Water programme, but also by private land owners. There is the potential for the release of more biological control agents if the conflicts of interest surrounding *Prosopis* are resolved (Zachariades et al., 2011). Between 1996 and 2008 *Prosopis* cover has increased by 35% despite R 435.5 million (US$ 42.7 million) being spent on controlling its spread (van Wilgen et al., 2012). Approximately 15,100 ha were cleared with this budget (van Wilgen et al., 2012). There is potential to look into other control mechanisms to improve management further, such as the control-by-utilisation approach applied in Kenya (Pasiecznik and Felker, 2006). These different methods each have advantages and disadvantages and management approaches are often are based on the population structure of invasive populations, the level of understanding of invasion, and development level of the country (van Wilgen et al., 2011; Shackleton et al., 2014). Baseline data on the population structures and impacts of *Prosopis* are needed to guide effective management in South Africa. This is particularly needed over large spatial scales, since previous studies have been site specific (Steenkamp and Chown, 1996; Dean et al., 2002; Ndhlovu et al., 2011; Schachtschneider and February, 2013).

Little attention has been given to determining the effects of invasive species on the recruitment, mortality and population stability of native plants across a representative range of environments. The use of size-class distributions (SCDs) provides a convenient method for assessing population trends in plants, and has been widely used in studies of rare, threatened and heavily utilised plants to guide in their management (Shackleton, 1993; Botha et al., 2004; Venter and Witkowski, 2010; Cousins et al., 2014). Few studies have used SCD curves to investigate the population structure of invasive alien populations, and even fewer have

applied this method to assess impacts of invasive plants on native species — most studies that have been done deal with *Prosopis* (van Klinken et al., 2006; de Oliveira et al., 2012; Muturi et al., 2013). SCD curves have the potential to provide important insights into the effects of invasive alien plants on native species population stability, and can inform management strategies based on population structures, recruitment and impacts.

2. Aims and objectives

a) Compare size-class distributions and population stability of *Prosopis* populations within different biomes in South Africa and with differing water availability. b) Determine whether invasive *Prosopis* populations are having an impact on the stability, population structure and mortality of native tree species.

3. Study site

The study was conducted at 11 sites in an area that covered three of South Africa's terrestrial biomes: the Succulent Karoo, the Nama Karoo and the Savanna (Fig. 1). Mean annual rainfall across the study area ranges from 150 to 450 mm (increasing towards the east); rainfall seasonality ranged from winter in the west to summer in the east with bimodal rainfall where they overlap (Dent et al., 1989). Rainfall across these sites has been highly variable over the last 10 years, but has tended to be close to the yearly average to slightly higher in the past three years at most sites (Agricultural Research Council, unpublished data). Altitudes range from 700 to 1300 m a.s.l. The most common land use in the area is livestock ranching and game farming.
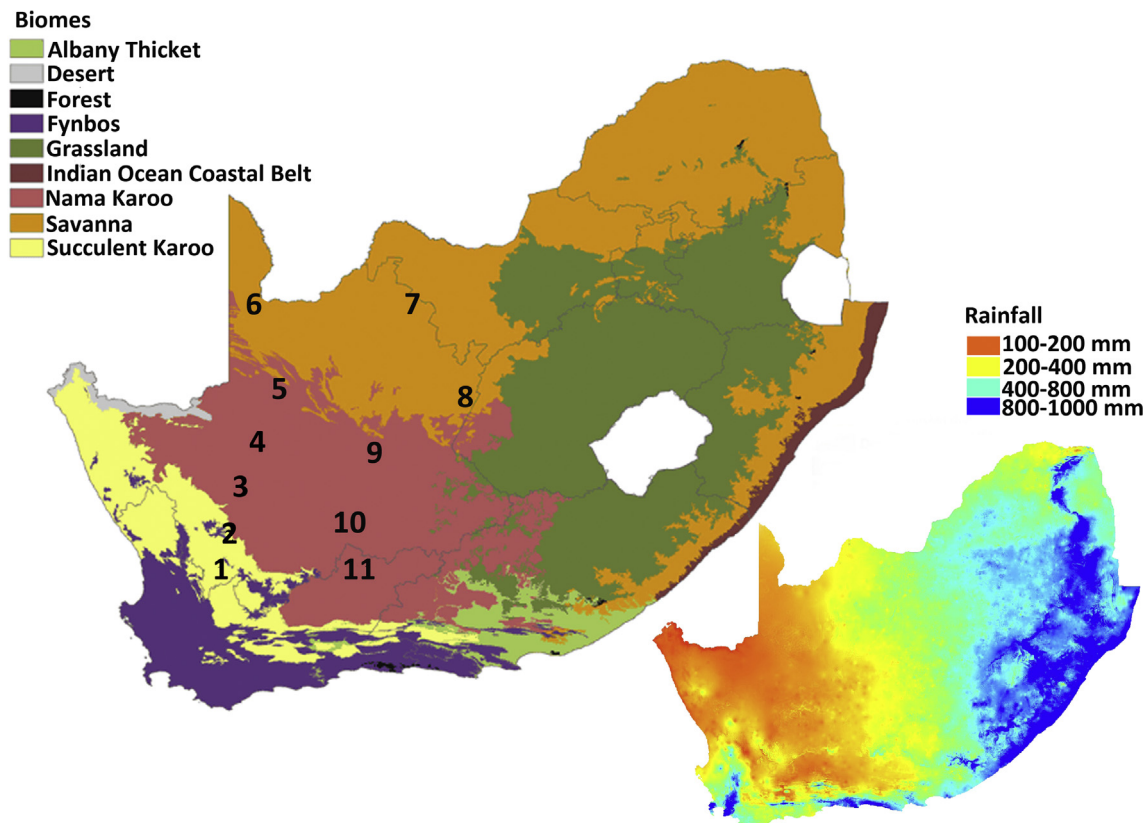

Fig. 1. The study area, showing biomes, mean annual precipitation and data collection points across South Africa: (1) Calvinia; (2) Loeriesfontein; (3) Brandvlei; (4) Kenhardt; (5) Upington; (6) Mier; (7) Seven; (8) Kimberley; (9) Prieska; (10) Carnavon; (11) Beaufort West.

4. Methods

4.1. Data collection

Data were collected between June and September 2013. At each site transects were established along rivers and alluvial plains where natural riverine forests were found in areas with varying levels of *Prosopis* stand density. Transects comprised three plots (10 × 10 m) placed every 50 m. Farmers were consulted on the past land practices on their farms to prevent placing transects in areas that were previously disturbed e.g. old flood irrigation fields or areas that were dammed. We also only worked on farms that had both invaded and non-invaded areas to ensure that major differences in land-use history did not confound our results.

In total 894 plots were surveyed across the 11 sites. In each plot all tree diameters were measured 30 cm above the ground and all trees were identified to species level (except *Prosopis*). This height was chosen because *Prosopis* and other native species often branch below breast height. For trees with multiple stems, all stem diameters were measured and summed to give a single tree diameter for the SCD analysis. Trees with diameters <1 cm were simply identified and counted. Diameters of all dead native tree species were measured and identified to species level based mainly on bark textures. *Prosopis* species were not identified to species level because most invasive stands in South Africa comprise hybrids that can only be accurately identified using molecular methods (Mazibuko, 2012). The different biomes and different river classes (Small Ephemeral, Large Ephemeral and Perennial) — indicative of water availability — were included to assess abiotic effects on *Prosopis* invasion structures.

4.2. Data analysis

Size-class distributions were constructed for *Prosopis* populations in different biomes and river classes. SCDs were also constructed for native tree species, and invasive alien *Tamarix ramosissima*, and were separated into two groups: (a) those with zero to low (ZL) *Prosopis* invasion (basal areas of <2 m²/ha); and (b) those with moderate to high (MH) *Prosopis* invasion (basal areas of >2 m²/ha). The value of 2 m²/ha was chosen because it formed a thresholds beyond which native species densities, basal areas, species richness and diversity decreased considerably (Shackleton et al., unpublished data). 723 plots (220 with no *Prosopis*) plots fell into the ZL class and 171 plots fell into the MH class. Only tree species with 10 or more records were included in the analyses. Kolmogorov–Smirnov tests were used to compare size-class distributions between trees found in the two *Prosopis*-density categories and to compare *Prosopis* SCDs in different biomes and river classes (Botha et al., 2002, 2004; Venter and Witkowski, 2010). Regressions were also run to assess the fit (R^2) of the SCD.

Prosopis and native tree population stability in areas with ZL invasion and MH *Prosopis* invasion were investigated by calculating the quotients between the numbers in successive size-classes (Harper, 1977). Quotients for the whole *Prosopis* population and populations in different biomes and along different river types were also calculated. Constant quotients indicate population stability and fluctuating quotients indicate unstable or episodically recruiting populations (Botha et al., 2002; Venter and Witkowski, 2010).

Population structures and stability of native trees found in ZL, and MH density invasions, and *Prosopis* populations in different biomes and on rivers in different types were further investigated using the Permutation Index (P-index) (Wiegand et al., 2000; Botha et al., 2004; Venter and Witkowski, 2010). The P-index compares the degree of deviation from a monotonic decline (Wiegand et al., 2000). Populations with monotonically declining populations will have a low P-index and those with discontinuous population structures will have a large P-index value (Wiegand et al., 2000; Venter and Witkowski, 2010).

Regression analyses were used to assess the relationship between the basal area of dead trees, density of dead trees and mean number of dead species in relation to different *Prosopis* invasion's basal areas.

5. Results

5.1. Prosopis populations

The overall *Prosopis* population in South Africa (Fig. 2) shows a positively skewed distribution with quotients fluctuating in the juvenile and large tree size-classes.

The shape of the SCD of *Prosopis* populations differed significantly between the three biomes (Succulent Karoo, Nama Karoo, Savanna) and along different types of rivers (small ephemeral, large ephemeral and perennial) (Kolmogorov–Smirnov test, $p < 0.001$) (Tables 1 and 2).

The Succulent Karoo biome had a higher proportion of trees in larger size classes, and the Nama-Karoo and Savanna had a higher proportion of juvenile trees and fewer in larger size classes (Fig. 3 and Table 1). The Nama Karoo has the smallest proportion of large trees. Perennial rivers had a much smaller percentage of juveniles in their populations than the two other river types and more trees in larger size classes (Fig. 3) which indicates less recruitment.

In areas with lower water availability the SCDs are dominated by smaller trees with a lack of larger trees in larger size-classes, whereas *Prosopis* populations with greater water availability
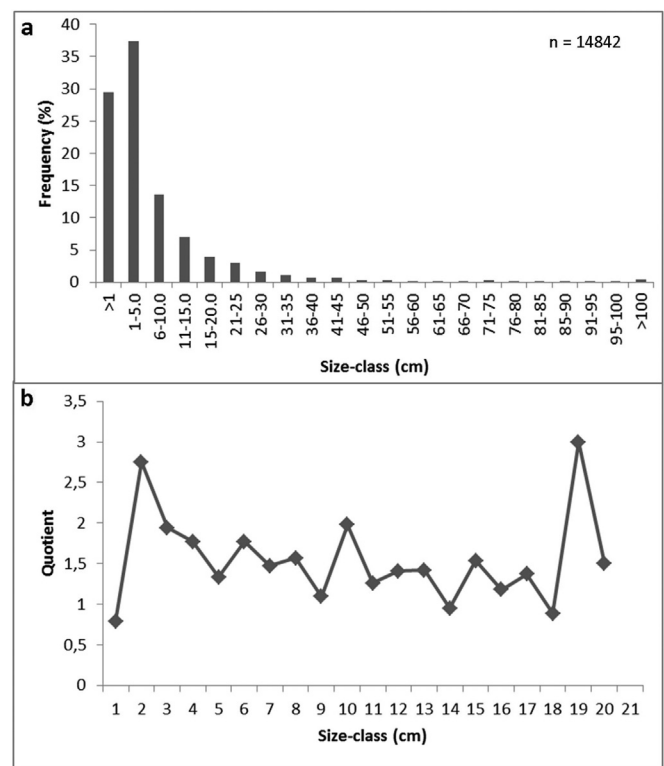

Fig. 2. Population structure of *Prosopis* spp. in South Africa: (a) size-class distributions (diameter at 30 cm above ground) and (b) quotients (ratios) of the numbers in different size classes.

Table 1
A comparison between the overall population structure of *Prosopis* spp. at the 11 sites across three different biomes and river types.

	% Juvenile	R^2	P-index	Kolmogorov–Smirnov against whole population
Total population	66	0.944	4	–
Biome				
Succulent Karoo	60.6	0.881	6	0.001
Nama Karoo	67.1	0.926	7	0.001
Savanna	65.7	0.850	5	0.001
River type				
Small Ephemeral	69.3	0.906	4	0.001
Large Ephemeral	69.5	0.926	5	0.001
Perennial	56.7	0.934	8	0.001

The percentage of juvenile plants in the whole *Prosopis* population was 66% which is indicative of high recruitment rates (Table 1). The Succulent Karoo and perennial rivers had slightly lower percentages of juvenile plants (Table 1). The high R^2 values illustrate that *Prosopis* populations fit the reverse J-shape in the SCD curve very well, indicating a stable populations with high recruitment (Table 1). Populations of *Prosopis* in the Nama Karoo fitted the reverse J-shape in the SCD curve better than populations in the other biomes. Quotients between successive size-classes show an unevenly distributed population, with high variation in small and large size-classes with more stability in the middle size-classes (Figs. 1 and 4). The Succulent Karoo and Nama Karoo showed low fluctuating quotients, whereas *Prosopis* populations in the Savanna were stable except when it came to the larger size-classes.

The P-index was fairly similar for the different biomes (Table 1). Populations in perennial rivers (high water availability) showed the

Table 2
Results of Kolmogorov–Smirnov tests comparing the size class distributions of *Prosopis* populations in different biomes and river types.

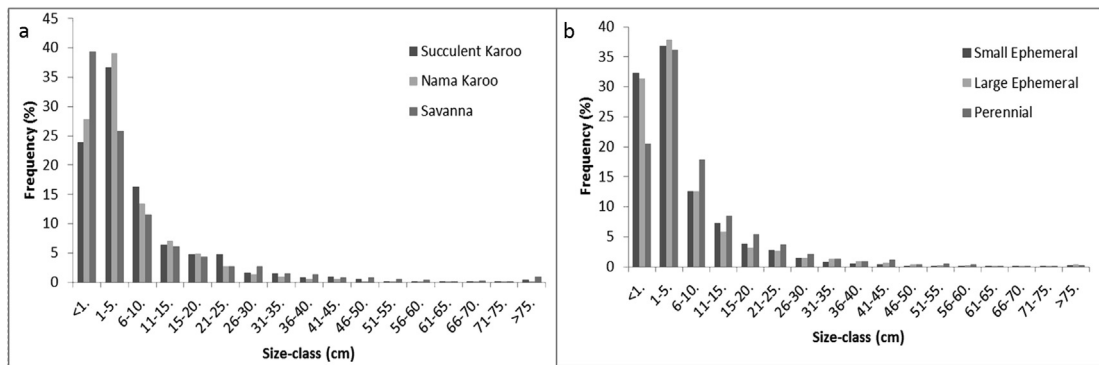| Biome	Succulent Karoo	Nama Karoo	Savanna	River type	Small Ephemeral	Large Ephemeral	Perennial
Succulent Karoo	–	0.001	0.001	Tributary	–	0.013	0.001
Nama Karoo	0.001	–	0.001	Ephemeral	0.013	–	0.001
Savanna	0.001	0.001	–	Perennial	0.001	0.001	–

Fig. 3. Size-class distributions of *Prosopis* (diameter at 30 cm above ground) in different biomes (a) and river types (b).

show fewer trees in smaller size-classes and more in larger size-classes.

highest amount of discontinuity. This may be because there were more large trees and fewer juveniles in these areas. Populations in small ephemeral rivers had the lowest P-index, meaning that they
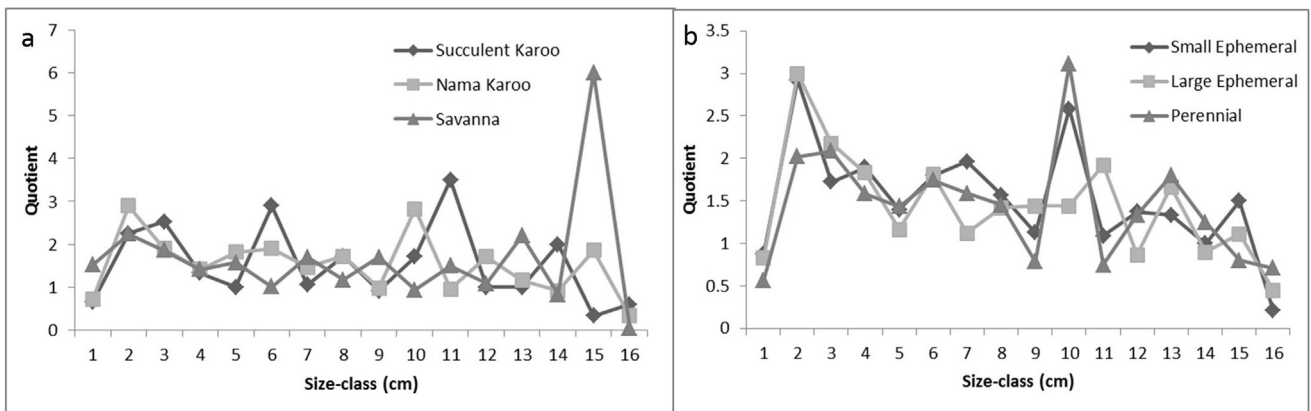

Fig. 4. Quotients indicating population stability between successive size-classes for *Prosopis* populations in different biomes and river types.
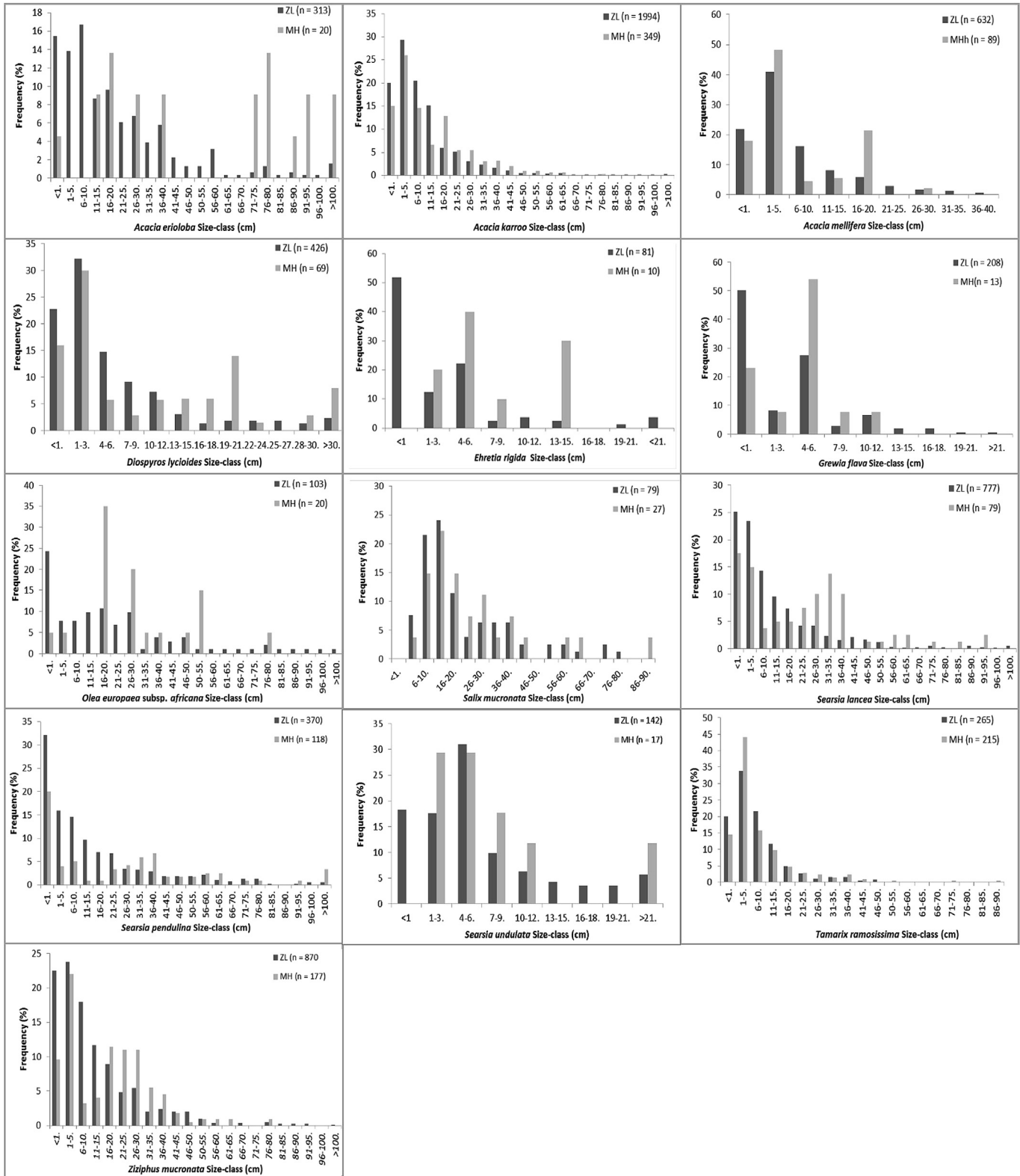
Fig. 5. Population structures of native and invasive alien trees found in areas with zero-low (ZL) and moderate to high (MH) levels of *Prosopis* invasion based on stem diameters 30 cm above the ground.

had the most stable monotonically declining population size structures. The fact that *P*-values in all areas are very low suggests that these *Prosopis* populations are undergoing regular recruitment

(i.e. SCD monotonically declining) areas across their range in South Africa.

5.2. Tree population trends under Prosopis invasion

All populations had positively skewed SCD curves (Fig. 5) with the native trees populations in ZL invasions fitting the reverse J-shape in the SCD better than tree populations in MH-density invasions highlighted by the R^2 values (Fig. 5; Table 3). Native tree populations under MH density invasions often had similar populations in the juvenile and adult populations but had lower numbers of trees in the middle size-classes (Fig. 5). About 60% of the native tree species found under ZL Prosopis invasion densities had significantly different SCDs population shapes compared to those under MH invasions (Kolmogorov–Smirnov $p < 0.05$) (Table 3). Prosopis is also having a negative impact on the population stability of another invasive alien tree in South Africa, T. ramosissima (Table 3).

Quotients fluctuated for all species but were generally more stable for areas with ZL density Prosopis invasion compared to MH density invasion (Fig. 6). The higher P-index for all species (except Ehretia rigida and Grewia flava which were the same) in sites with MH density invasions compared to ZL Prosopis invasion density indicates a higher level of discontinuity within populations (Table 3) and, therefore, a less stable population structure.

5.3. Effects of Prosopis invasion tree species mortality

As Prosopis basal area increased the basal area of dead native trees increased significantly ($p < 0.001$) (Fig. 7). Approximately 36% of the basal area mortality of woody plants is explained by Prosopis invasion. Larger Prosopis basal areas were also related to a significant increase in the number of dead trees/ha and the mean number of dead plant species per 100 m^2 at different Prosopis basal areas ($P < 0.001$).

6. Discussion

6.1. Prosopis population structures

The data on population structure of invasive Prosopis stands in South Africa illustrates strong and sustained recruitment, with stable reverse J-shaped SCD structures (Table 1, Figs. 2 and 3). However, there are differences between biomes and river classes which show that abiotic factors are influencing Prosopis population structure in South Africa. Interestingly, Prosopis populations along perennial rivers (Orange River), with readily available water, show lower proportions of juveniles in their population structures. This may be because Prosopis trees are larger and have higher mean basal areas, due to high water availability, which leads to greater intraspecific competition (Shackleton et al., unpublished data), thus limiting seedling establishment. The Succulent Karoo also had higher basal area Prosopis populations and showed lower percentage juvenile populations (Shackleton et al., unpublished data). Populations with lower basal area densities had a higher percentage of juveniles in their populations, and were often found in more arid areas.

Prosopis population structures in this study show greater percentage juveniles than Australia, which is indicative of higher recruitment rates (van Klinken et al., 2006), but similar to that of invasive populations in Kenya (Muturi et al., 2013) and those at early stages of invasion in Brazil (de Oliveira et al., 2012). Other studies in South Africa (at Riemvasmaak, to the west of Upington — outside our study area) found Prosopis populations to be lacking larger individuals (SDC of >1–7) but showing good reverse J-shaped population structures (Hoffman et al., 1995). The Riemvasmaak population was thought to be in the early stages of invasion which would account for the lack of larger trees (Hoffman et al., 1995). These findings confirm Van den Berg's (2010) conclusions that there has been a rapid recruitment and significant increases in the extent of Prosopis invasions between 1974 and 2007.

The findings also suggest that Prosopis populations are not undergoing self-thinning and that intraspecific competition is limiting trees in larger size-classes from being more dominant in South Africa (all the invasive stands were over 15 years old and many of them over 50 years old) (Fig. 2). This leads to highly positively skewed population structure with a lack of larger individuals. Muturi et al. (2013) also noted a lack of self-thinning in invasive Prosopis stands in Kenya. However, Prosopis population structures in Australia represent more of a normal curve shape, illustrating slower recruitment with moderate sized trees being dominant (van Klinken et al., 2006). Chinninimani (1998) suggests that after 50–60 years Prosopis invasions in India recruit more slowly, die back and thin out allowing native trees to return, with larger trees remaining dominant. The same thinning of native 'weedy' Prosopis has been found in populations in the USA and is also a common successional phenomenon in other semi-arid native 'weedy' tree species (Archer, 1995; Shackleton et al., 2013).

We do not understand the mechanism behind this self-regulation, and why it does not seem to apply to places like South Africa. Our findings highlight the need for improved control methods as Prosopis in South Africa shows high recruitment rates and rapid spread (Fig. 2; Table 1; Van den Berg, 2010). There is also a need to understand the ecology of the species by adding a temporal component to guide management decisions — e.g. will Prosopis in South Africa eventually go through this self-thinning as suggested by Chinninimani (1998)? If so this could have implications for management in the future.

6.2. The impacts of Prosopis on native tree populations

The analysis of population SCDs suggests that Prosopis invasions are having a negative effect on native tree population structures and stability. In most cases native tree species recruitment is higher in non-invaded areas and indicators of population stability (P-index and quotients) were better in areas with low invasion densities relative to areas with moderate-high invasion (Figs. 5 and 6; Table 3). However, it must be noted that recruitment in arid ecosystems is stochastic, and is highly dependent on above-average annual precipitation over a few seasons (Chesson et al., 2004). In most of the Northern Cape rainfall was slightly above average in the three years preceding the study (Agricultural Research Council,

Table 3
Population parameters for native trees and the alien Tamarix ramosissima at sites with (zero to low) ZL and (moderate to high) MH levels of Prosopis invasion.

Species	ZL invasion		MH invasion		Kolmogorov–Smirnov
	R^2	P-index	R^2	P-index	p-Value
Acacia erioloba	0.780	40	0.006	138	0.01
Acacia karroo	0.886	18	0.856	23	0.007
Acacia mellifera	0.964	2	0.417	10	0.946
Diospyros lycioides	0.794	12	0.239	30	0.005
Ehretia rigida	0.723	12	0.181	12	0.640
Grewia flava	0.853	4	0.154	4	0.264
Olea europaea subsp. africana	0.735	32	0.139	66	0.01
Salix mucronata	0.217	50	0.231	54	0.9
Searsia lancea	0.831	37	0.596	58	0.002
Searsia pendulina	0.873	26	0.341	74	0.001
Searsia undulata	0.709	6	0.057	16	0.643
Tamarix ramosissima	0.898	10	0.786	28	0.001
Ziziphus mucronata	0.891	33	0.631	40	0.009

unpublished data) which may account for the high number of *Prosopis* juveniles and the high juvenile populations for many native species. However, there has been high rainfall variability over the last 10 years, which may be contributing to the stochastic population's structures. There is seedling establishment for most native species and the larger native trees are present in invaded areas. However, the middle size classes for most native tree populations were lower in MH density *Prosopis* invasions (Fig. 5). *Acacia erioloba*, *E. rigida* and *Olea europaea* subsp. *africana* showed very little to no recruitment in areas invaded with *Prosopis* but had

juveniles in areas with low *Prosopis* invasion (Fig. 5). *Salix mucronata* was the only species with no juveniles in areas with both low and moderate to high invasion. This suggests that most native tree seedlings can initially establish in invasive *Prosopis* stands but are soon outcompeted. It also shows that large well-established trees can compete with *Prosopis*, although they are likely to die back eventually (Figs. 5 and 7). Native tree seedlings were also found in invasive *Prosopis* stands in Kenya, with a lack of native trees in the middle and large size-classes (Muturi et al., 2013). This illustrates the negative impacts of *Prosopis* on native species population
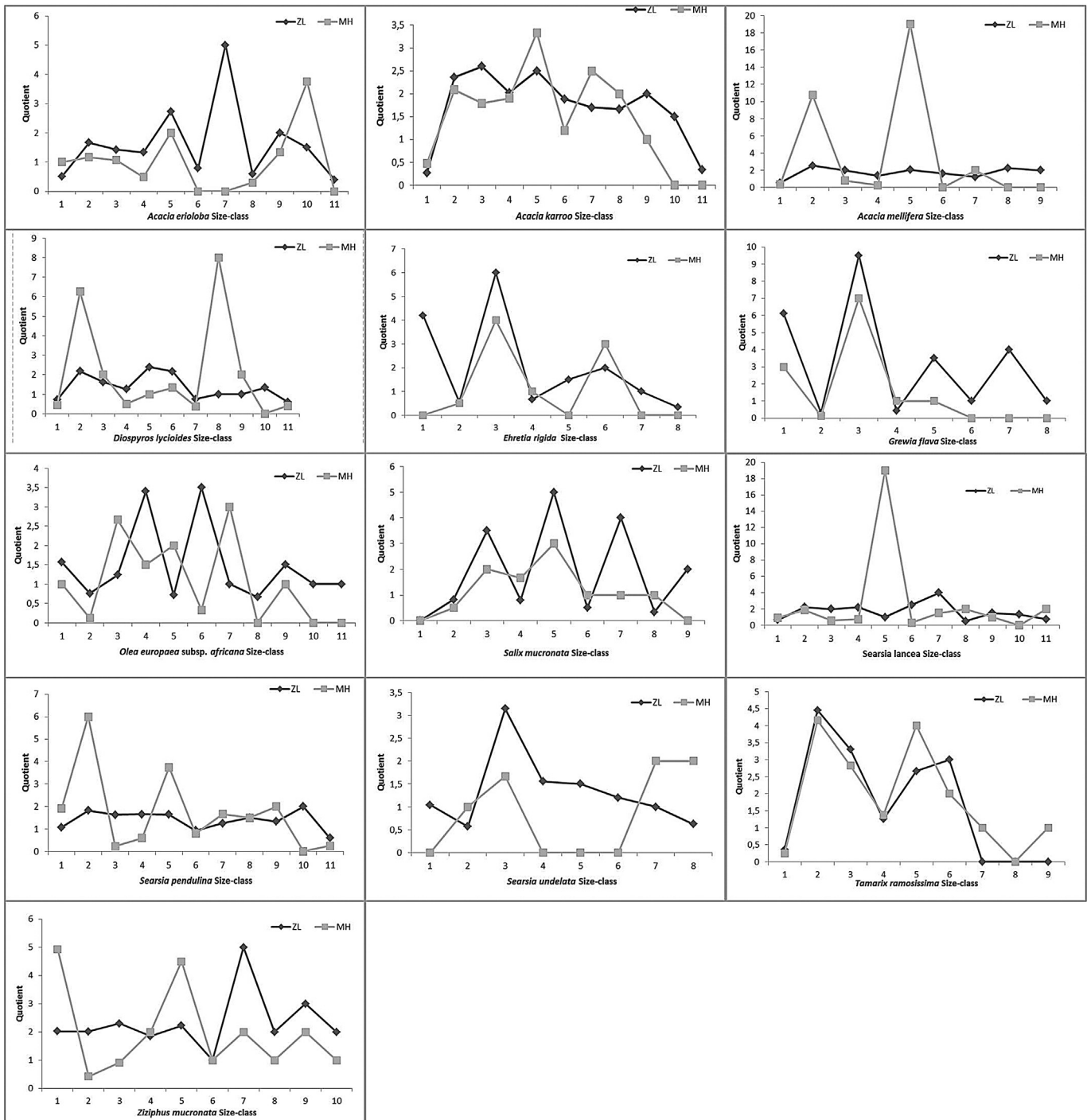

Fig. 6. Quotients comparing native tree population stability between successive size-classes in areas of zero-low (ZL) and moderate to high (MH) levels of *Prosopis* invasion.
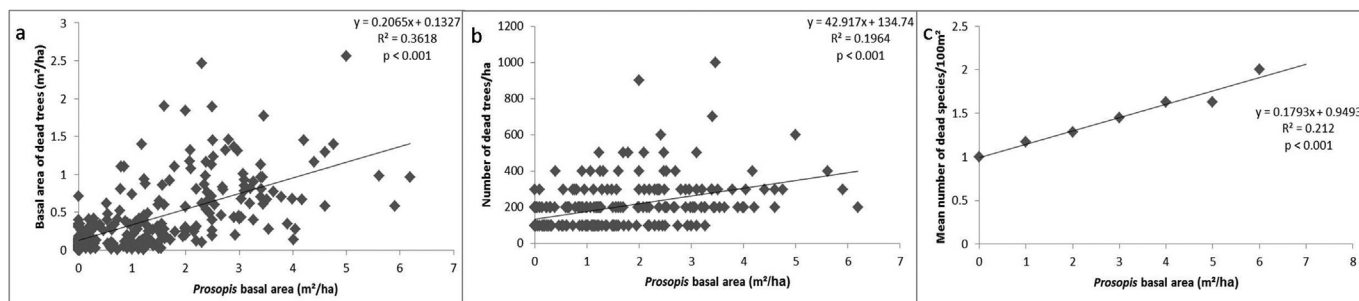
Fig. 7. The effect of *Prosopis* basal area on (a) dead tree basal area (b) number of dead trees (c) mean number of dead species.

stability in South Africa and also in other parts of Africa (Muturi et al., 2013). The results suggest that interspecific competition for limited resources between *Prosopis* and native trees is causing increased native tree mortality (Fig. 7). Mascaro et al. (2008) also show many more dead stems in areas with tree invasions as opposed to uninvaded areas, as well as an overall lower recruitment in Hawai'i. In Brazil, *P. juliflora* invasions reduce native seedling growth rates by half and cause increased seedling mortality of native woody plants (de Souza Nascimento et al., 2014). The increased native tree mortality and negative impact on population structure is of particular concern for protected and keystone species in South Africa like *A. erioloba* (Milton and Dean, 1995; Seymour et al., 2003) (Fig. 5). *Prosopis* invasions also negatively impact *A. erioloba* populations due to increased competition for ground water, as they have deeper root systems and are causing substantial die back of this species (Schachtschneider and February, 2013). Interestingly, *Prosopis* also seems to be slowly out-competing another invasive alien tree species — *T. ramosissima*.

The formation of these dense monospecific stands of *Prosopis* dominated by small to moderate sized trees in invaded areas as seen in South Africa is particularly problematic (Fig. 2). This is because these *Prosopis* thickets reduce grazing potential, access to land, and produce small shrubby trees that provide no little or no goods and services for human use (Mwangi and Swallow, 2005; Shackleton et al., 2014). The loss of native trees due to *Prosopis* invasion also has negative effects on other species like birds, due to reduction of suitable nesting sites and food availability (Dean et al., 2002). *Prosopis* invasion also affects local human communities who rely on many specific natural resources from native trees, for example *A. erioloba* is extremely popular for fuelwood and fodder (Powell, 2001; Stave et al., 2007).

6.3. Prosopis management

Our findings illustrate the need for the management of *Prosopis*, as it is impacting native biodiversity and recruiting rapidly. The insights on *Prosopis* population structures discussed here will be useful for guiding management. *Prosopis* is often managed using a control-through-utilisation approach in developing countries, as this provides valuable resources (Pasiecznik and Felker, 2006; Kazmi, 2009; Choge et al., 2012). Having an understanding of the SCD of *Prosopis* populations is essential when considering this approach as it can inform managers how many trees can be harvested and allow for the calculation of potential profits. One suggestion is to produce timber products such as furniture and flooring using invasive *Prosopis* trees in Africa, which is commonly done with *Prosopis* in its native range. However, trees need to be greater than 20 cm in diameter for this (Felker, 2002). The *Prosopis* SCD (Fig. 2) shows that trees of this size-class are uncommon in invasive stands in South Africa. Areas in Kenya also lack larger trees (Muturi

et al., 2013). This suggests that management of *Prosopis* through timber extraction is not a viable option in South Africa and possibly in other parts of Africa such as Kenya. However, there is potential for the use and management of *Prosopis* to create charcoal, bio-char and ethanol, which can be made from smaller trees (Kazmi, 2009). Localised small-scale power generation is also viable for these smaller sized trees and power plants are currently being built in Kenya to aid local development and try and reduce *Prosopis* invasion cover (Shackleton et al., 2014).

At a local level, having information on invasive species population structures can greatly aid management. Currently, planning for clearing projects conducted by the Working for Water programme is based on ad hoc estimates of population structure based on crude visual estimation. Knowledge of the SCDs of populations and having this baseline data will enable Working for Water to better calculate clearing costs. Information on invasive *Prosopis* population structure is also needed for monitoring, to assess the effectiveness of management strategies. This baseline information is also needed if adaptive management is going to be implemented to track project success.

7. Conclusions and priorities for future research

Prosopis invasions in South Africa are impacting the population stability of many native tree species. These trees provide important ecosystem services in the arid and semi-arid parts of South Africa and therefore *Prosopis* invasions need to be managed to mitigate against the loss of these services. This research can be taken further by adding a temporal component; this will involve re-visiting sites to collect data to facilitate population growth modelling and elasticity analysis which would allow for more detailed comparisons between different populations and for the calculation of population growth rates (Goluboc et al., 1999). There is also a need for further research on the impacts of *Prosopis* invasions on species — especially, rare, endemic and endangered species, such as the Riverine rabbit (*Bunolagus monticularis*). A national strategy is needed to guide the management of invasive populations of *Prosopis* in South Africa and in other regions where it is invasive, and an understanding *Prosopis* population structure and the impacts of invasion on native tree species will help to facilitate this.

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