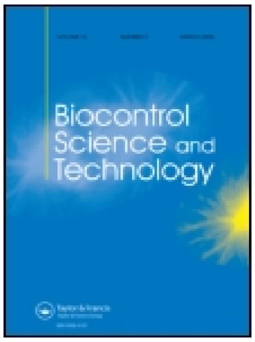

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RESEARCH ARTICLE

Prioritisation of potential agents for the biological control of the invasive alien weed, *Pereskia aculeata* (Cactaceae), in South Africa

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Pereskia aculeata Miller (Cactaceae) is an invasive alien species in South Africa that is native in Central and South America. In South Africa, *P. aculeata* outcompetes native plant species leading to a reduction in biodiversity at infested sites. Herbicidal and mechanical control of the plant is ineffective and unsustainable, so biological control is considered the only potential solution. Climatic matching and genotype matching indicated that the most appropriate regions in which to collect biological control agents were Santa Catarina and Rio de Janeiro provinces in Southern Brazil. Surveys throughout the native distribution resulted in 15 natural enemy species that were associated with the plant. Field host range data, as well as previous host plant records, were used to prioritise which of the species were most likely to be suitably host specific for release in South Africa. The mode of damage was used to determine which species were most likely to be damaging and effective if released. The most promising species prioritised for further study, including host specificity and impact studies, were the stem-wilter *Catorhintha schaffneri* Brailovsky & Garcia (Coreidae); the stem boring species *Acanthodoxus machacalis* Martins & Monné (Cerambycidae), *Cryptorhynchus* sp. (Curculionidae) and *Maracayia chlorisalis* (Walker) (Crambidae) and the fruit galler *Asphondylia* sp. (Cecidomyiidae). By prioritising the potential biological control agents that are most likely to be host-specific and damaging, the risk of conducting host specificity testing on unsuitable or ineffective biological control agents is reduced.

Keywords: climatic matching; genotype matching; weed biological control; agent selection; natural enemies

1. Introduction

Pereskia aculeata Miller (Cactaceae) is a primitive creeping cactus native to Central and South America that has become a problematic alien invasive in South Africa (Klein,1999; Leuenberger, 1986; Moran & Zimmerman, 1991; Paterson et al., 2011b). The first record of the species in South Africa was at the Cape Town Botanical Garden in 1858 (McGibbon, 1858), but it was not until 1979 that the negative impacts of the weed were recognised and the plant was declared an Invasive Alien Plant (Proclamation No. R.35, 1979). *P. aculeata* is now widespread in South Africa occurring in seven of the nine provinces in the country (Figure 1). The plant is

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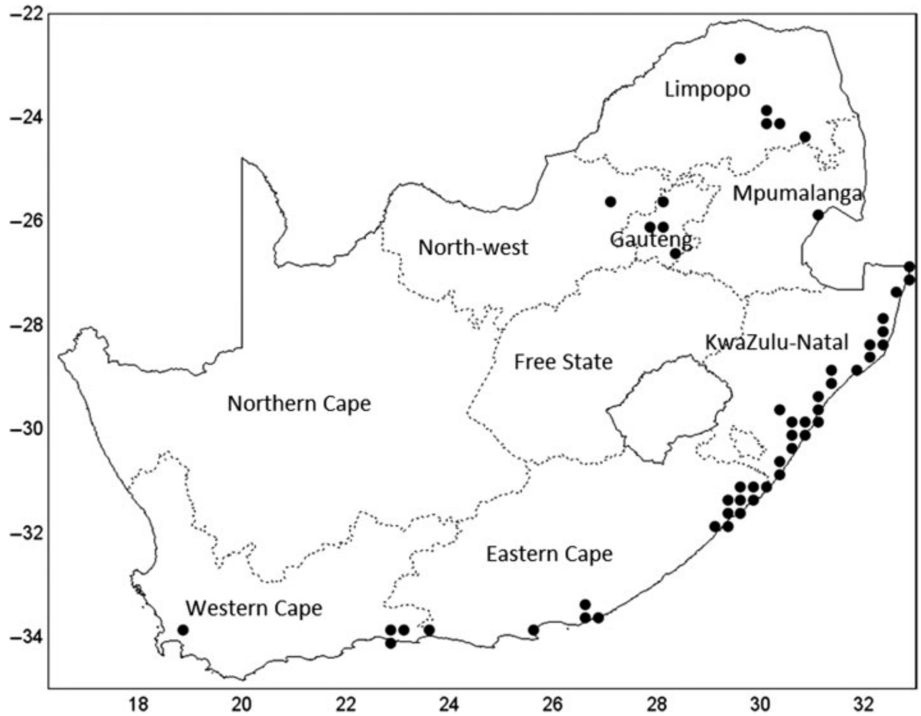

Figure 1. The distribution of *P. aculeata* in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria).

most prolific and damaging along the eastern coastal region of the country where the climate is subtropical (Figure 1).

Pereskia aculeata outcompetes native plant species leading to a reduction in native plant biodiversity (Paterson, Coetzee, Downie, &Hill, 2011a). The *P. aculeata* population in South Africa produces viable seeds that are spread when the fruits are eaten by birds or bats (Campbell, 1988). This enables the plant to invade undisturbed areas, so it is often damaging in otherwise pristine environments and should therefore be considered a ‘driver’ of biodiversity loss rather than a ‘passenger’ of disturbance (MacDougall & Turkington, 2005). Asexual reproduction, through the growth of broken fragments of stems which readily root, as well as the sprawling growth habit of the plant leads to high densities within infested sites (Paterson et al., 2011a).

Mechanical and herbicidal controls are ineffective and unsustainable against *P. aculeata* making biological control the only potential solution (Moran &Zimmermann, 1991). One biological control agent, *Phenrica guerini* Bechyné (Chrysomelidae), was released in 1994 but its impact has been limited (Klein, 1999, 2011; Paterson et al., 2011b). New biological control agents are thus required in order to reduce *P. aculeata* infestations in South Africa to appropriate levels (Paterson et al., 2011a), so surveys in the plant’s native range were conducted in order to identify new potential biological control agents.

Pereskia aculeata has a disjunct native distribution, with northern Venezuela and the Caribbean comprising the northern region of the native distribution and northern Argentina, south and south-eastern Brazil comprising the southern native distribution (Figure 2) (Leuenberger, 1986). Surveys for potential biological control agents have been conducted in both regions of the native distribution, but significantly more sampling effort has been concentrated in the southern region in terms of time spent in the area and the number of sites surveyed (Figure 3). From the phytophagous species identified from surveys in the native distribution of *P. aculeata*, the most promising species should be prioritised for further research including host specificity testing and impact studies.

Prioritising the most promising potential biological control agents from data collected during surveys in the weed's region of origin is an essential component of biological control programmes (Van Klinken & Raghu, 2006). There are often large numbers of herbivorous arthropod species associated with plants (Balciunas,

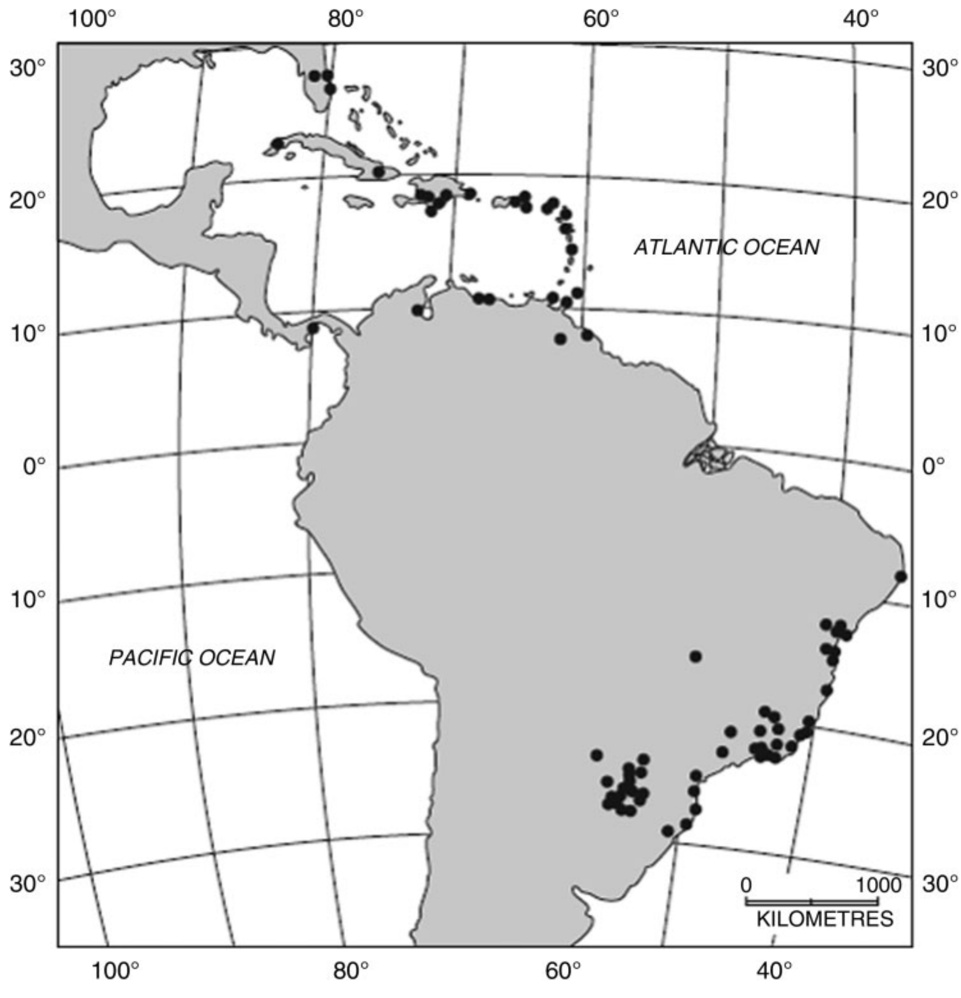

Figure 2. The native distribution of *P. aculeata* (from Leuenberger, 1986).

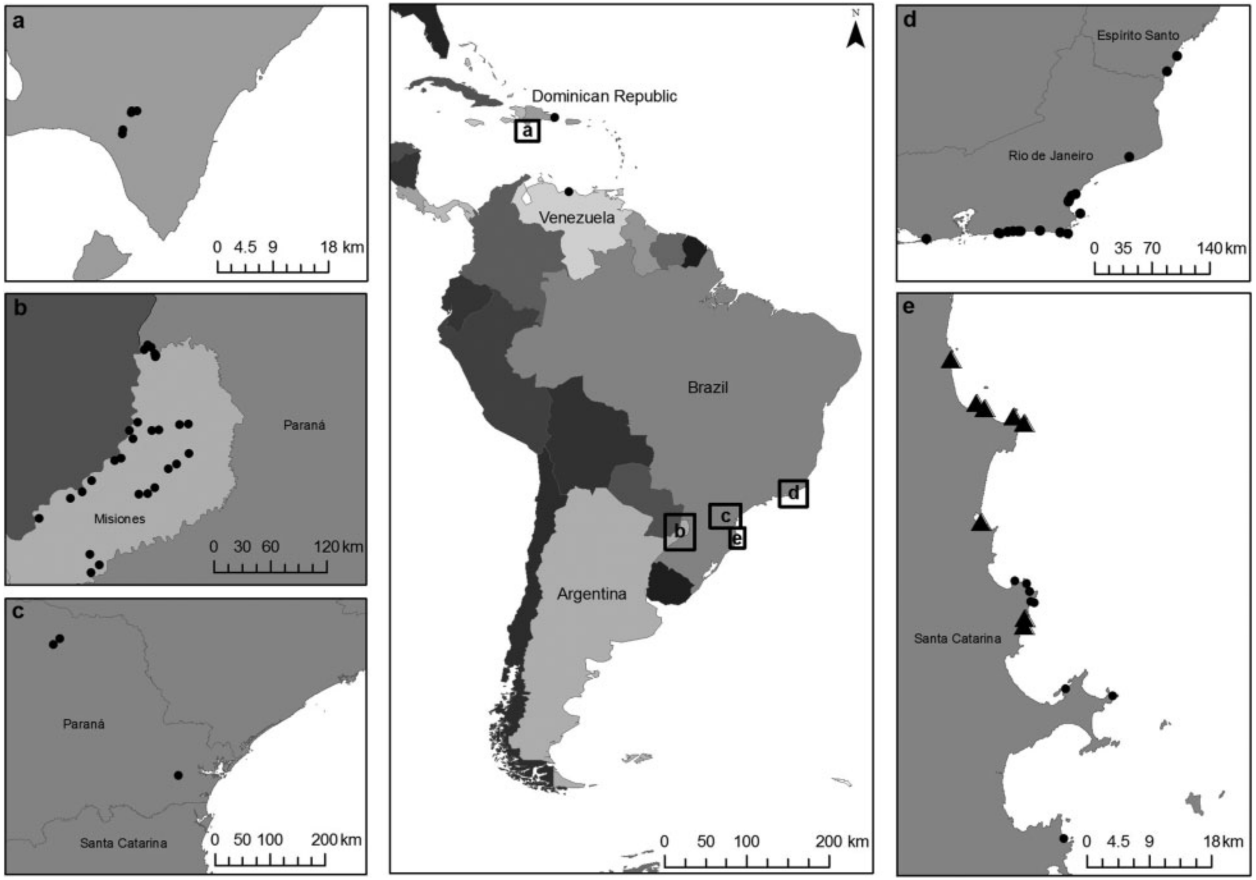

Figure 3. Sites surveyed for natural enemies on *P. aculeata*. Black dots indicate sites visited during surveys while triangles indicate the eight long term monitoring sites (Figure 5e).

Burrows, & Purcell, 1995; Fontes, Habeck, & Slansky, 1994; Gillett, Harley, Kassulke, & Miranda, 1991; Harley et al., 1995; Kennedy & Southwood, 1984; Palmer, 1987; Palmer & Pullen, 1995; Syrett, Fowler, & Emberson, 1996) making host specificity testing of all the potential biological control agents infeasible. In the case of *Lantana camara* L. (Verbenaceae), for example, 550 phytophagous species were recorded on the plant during surveys (Palmer & Pullen, 1995) but only 36 species have been released as biological control agents worldwide (Julien & Griffiths, 1998). The cost of conducting host specificity testing on a potential biological control agent was estimated at USD $460 000 in 1997 and each species was estimated to take 3 scientist years, so the costs of conducting host specificity testing on agents that are not suitable are high and should be avoided (McFadyen, 1998). The most promising of the potential biological control agents should therefore be determined prior to host specificity testing, although the predicted host range of the potential biological control agent should be taken into account during the prioritisation process. Systems for prioritising biological control agents have been proposed, but the data required for prioritisation include information that is difficult to obtain without detailed studies of the insect's life cycle, levels of parasitism and host specificity (Goeden, 1983; Harris, 1973). These systems can be used to prioritise potential biological control agents after laboratory-based studies have been concluded, but are not appropriate for prioritising potential biological control agents for further research based on data from surveys in the weed's region of origin.

Climatic matching and genotype matching can be used to select suitable biological control agents that are likely to establish and maintain healthy populations after release (Goolsby et al., 2006; Paterson, Downie, & Hill, 2009; Robertson, Kriticos, & Zachariades, 2008). Natural enemies found in areas of the native distribution where climatic conditions are similar to those in the introduced distribution are more likely to establish and persist as biological control agents because local adaptations to the climatic conditions in the native distribution will be suitable for the new environment in the introduced range (Robertson et al., 2008). Similarly, natural enemies found feeding on plants in the native distribution that are genetically similar to those in the introduced distribution are likely to have local adaptations for feeding on the invasive plant genotypes (Goolsby et al., 2006).

Field host range data can also be used to prioritise which insects are likely to be suitable for biological control. Field host range is the least conservative measure of specificity that can be determined prior to the release of a biological control agent (Syrett & Emberson, 1997), so any feeding on non-target plants recorded in the native distribution strongly suggests such plant species will be acceptable hosts in the introduced distribution. Insects found feeding on plant species outside of the target plant's family are therefore likely to be polyphagous and unsuitable for biological control. Conversely, insect herbivores found on the target weed, but not on closely related plant species growing sympatrically, are more likely to be suitably host-specific.

The mode of damage inflicted by a natural enemy can be used to predict whether the species is likely to be suitably damaging if released. Natural enemies that damage the vascular tissue or mechanical support tissue of the plant are more likely to be effective biological control agents than those that damage the leaves, seeds or flowers (Goeden, 1983; Harris, 1973). Although many seed, flower or fruit feeding biological control agents have been successful at reducing invasive alien plant populations (e.g. Hoffmann & Moran, 1999; Story, Smith, Corn, & White, 2008), seed or fruit attacking agents alone are unlikely to significantly reduce *P. aculeata* infestations due to the plant's ability to reproduce asexually. Species that damage the vascular tissue or structural support tissue of *P. aculeata* should therefore be considered promising for biological control.

When prioritising the most promising potential biological control agents for a weed species it is important that all the natural enemies of the target weed are considered (Van Klinken & Raghu, 2006). Species accumulation curves can be used to determine if all associated phytophagous insects were sampled. If sampling effort has been adequate to sample all the species associated with the target weed, it is unlikely that any new potential biological control agents would be encountered if further surveys were conducted.

The aim of this study was to identify potential biological control agents for *P. aculeata* and to prioritise which potential agents are most likely to be suitable for release in South Africa. The likelihood that establishment would be successful and that high population densities would be reached was inferred from climatic matching and genotype matching. The probability that a species would be suitably host-specific for release in South Africa was determined from host plant records and field host range. The probability that a species would be suitably damaging for release was determined from the mode of damage of each natural enemy species. The intention of prioritisation was to select the most promising of the species for further study and thus reduce the probability that resources would be wasted on studying species that are unlikely to be suitable for biological control.

2. Methods

2.1. Climatic matching and genotype matching

Selection of the most appropriate regions of the native distribution in which to collect natural enemies was determined through climatic matching and genotype matching. Climatic matching was performed using MaxEnt (Phillips, Andean, & Schapire, 2006; Phillips, Dudik, & Schapire, 2004) to identify regions in the native distribution of *P. aculeata* that were climatically most similar to those in the introduced distribution in South Africa. Locality data were sourced from the Southern African Plant Invaders Atlas (SAPIA) database, ARC-Plant Protection Research Institute (Henderson, 2007). The plant's distribution in South Africa is believed to be limited by climate (Campbell, 1988) and the plant has been in South Africa for over 150 years (McGibbon, 1858), so the distribution in South Africa is believed to have reached its full extent. Suitable bioclimatic predictor variables associated with the distribution of *P. aculeata* were selected and downloaded from the WORLDCLIM database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These data included an uncorrelated range of averages, outliers and seasonal variations (Hijmans et al., 2005). The genetic similarity of plants from the various regions of the native distribution to the South African *P. aculeata* population has been determined (Paterson et al., 2009). Regions from which the plants most closely related to those in South Africa were sampled are considered suitable regions from which to collect, while regions where more distantly related plants were sampled are considered less suitable (Paterson et al., 2009).

2.2. Sampling

Sampling for natural enemies of *P. aculeata* was conducted at 77 sites during 82 days of field work on nine field trips to the native distribution conducted between 1988 and 2013 (Table 1). Many sites and regions were visited more than once during different times of the year to account for seasonal variability of natural enemies (Table 1). All phytophagous insects found on *P. aculeata* were collected and immatures were reared to adults for identification. Species that were only recorded once at a single site and species that were not feeding on the plant were considered incidental visitors and have been excluded. Voucher specimens of insect species are housed at the South African National Collection (ARC-PPRI), Pretoria and referred to by Rhodes University accession numbers (AcRH) (Table 2). Voucher specimens were identified to the lowest taxonomic level possible by experts at the South African National Collection (ARC-PPRI), Pretoria and then sent to local and international experts in the relevant taxonomic group if necessary. If identification to the species level was possible then a thorough literature review was conducted for any host plant records for that species.

In addition to the surveys conducted throughout the native distribution, monthly monitoring was conducted over a period of 19 months at eight sites in Santa Catarina Province, Brazil (Figure 3). These long-term monitoring sites were included in order to sample any seasonal variation in natural enemy composition. Santa Catarina Province was selected above other regions for long-term monitoring because climatic and genetic matching indicated that this was an appropriate region in which to collect potential biological control agents (Paterson et al., 2009) and because a higher number of natural enemy species was found in this region than in any other region (Table 3).

2.3. Field host range

Field host range data were collected by surveying for phytophagous insects on closely related plant species growing sympatrically with *P. aculeata*. *Rhipsalis cereuscula* Haworth (Cactaceae) is a cactus species that grows sympatrically with *P. aculeata* at six of the sites in Santa Catarina Province, Brazil. It is also a close relative to the only cactus species that is considered native in South Africa, *Rhipsalis baccifera* (J. Müller) Stern (Dyer, 1975). At each site, both *P. aculeata* and

Table 1. A summary of the surveys for natural enemies of *Pereskia aculeata* in the native distribution giving the number of sites visited in each province, the number of days spent sampling in each province and the months in which each province was visited.

Country	Province	Number of sites	Days	Months
Dominican Repbulic	–	6	11	May; Nov
Venezuela	–	1	1	Sep
Brazil	Rio de Janeiro	19	24	Feb; Mar; Aug; Oct
Brazil	Espirito Santo	2	2	Mar
Brazil	Parana	3	3	Jan; Mar; Nov
Brazil	Santa Catarina	17	24	Jan; Mar; May; Oct; Nov
Argentina	Misiones	29	17	Jan; Aug; Oct; Nov

Table 2. The phytophagous insect species associated with *P. aculeata* in the native distribution.

Species	RH Acc. No.	Host specificity	Damage	Climatic matching	Genetic matching
Hemiptera					
Catorhintha schaffneri (Coreidae)	911	+	+ Shoots	+	+
Membracis sp. (Membracidae)	787	?	– Leaves	+	+
Bolbonota sp. (Membracidae)	803	?	– Leaves	+	–
Aetalion reticulatum (Aetalionidae)	798,799	–	– Stems	+	–
Coleoptera					
Acanthodoxus machacalis (Cerambycidae)	870	?	+ Stems	+	+
Adetus analis (Cerambycidae)		–	+ Stems	+	–
Xyleboru saffinis (Scolytidae)		–	– Stems	+	–
Phenrica guerini (Chrysomelidae)		+	+ Leaves	+	+
Cryptorhynchus sp. (Curculionidae)	849–853	+	+ Stems	+	–
Diptera					
Asphondylia sp. (Cecidomyiidae)		?	± Fruits	+	+
Lepidoptera					
Porphyrosela sp. (Gracillariidae)	747,748	–	– Leaves	+	+
Loxomorpha cambogialis (Pyralidae)		–	– Leaves	+	+
Maracayia chlorisalis (Crambidae)	744–746	?	+ Shoots	+	+
Hymenoptera					
Pseudopachylosticta subflavata (Cimbicidae)	755	–	– Leaves	+	–
Bruchophagus sp. (Eurytomidae)	749,750, 783	?	– Leaves	+	+

Note: The Rhodes University (RH) accession numbers are given for specimens housed at the South African National Collection of Insects (ARC-PPRI). A positive or negative was allocated to each species for each prioritisation criterion. The part of the plant damaged by each insect species is given under the damage criteria. Question marks are used where insufficient data about field host range of the species exist.

R. cereuscula plants were searched for externally feeding insects and then 10 stems of *P. aculeata* and 10 equivalent stems of *R. cereuscula* were dissected in order to observe any internally feeding larvae.

Talinum paniculatum Gaertner (Portulacaceae) and *Anredera cordifolia* (Ten.) Steenis (Basellaceae) have similar mucilaginous leaves to those of *P. aculeata* and are in closely related families to the Cactaceae (Wallace & Gibson, 2002). Both species are common in Southern Brazil and Misiones Province, Argentina. *Talinum paniculatum* and *A. cordifolia* were surveyed whenever encountered and were always surveyed if growing sympatrically with *P. aculeata*.

Table 3. The phytophagous insect species associated with *Pereskia aculeata* in the native distribution.

Species	Dominican Republic		Venezuela		Rio de Janeiro		Espirito Santo		Paraná		Santa Catarina		Misiones	
	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance
Hemiptera														
Catorhintha schaffneri (Coreidae)					3	++					2	+++		
Membracis sp. (Membracidae)					3	++								
Bolbonota sp. (Membracidae)											3	++		
Aetalion reticulatum (Aetalionidae)									1	+++			1	+++
Coleoptera														
Acanthodoxus machacalis (Cerambycidae)					5	+++					1	+		
Adetus analis (Cerambycidae)											6	++		
Xyleborus affinis (Scolytidae)											8	++		
Phenrica guerini (Chrysomelidae)					6	++								
Cryptorhynchus sp. (Curculionidae)											7	+++		
Diptera														
Asphondylia sp. (Cecidomyiidae)					1	+	1	+			3	+	1	+
Lepidoptera														
Porphyrosela sp. (Gracillariidae)					7	++					7	++	4	++

Table 3 (*Continued*)

Species	Dominican Republic		Venezuela		Rio de Janeiro		Espirito Santo		Paraná		Santa Catarina		Misiones	
	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance	No. sites	Relative Abundance
Loxomorpha cambogialis (Pyralidae)	5	+			8	++	1	+	2	+++	8	++	1	+
Maracayia chlorisalis (Crambidae)	6	+	1	+	7	++			1	++	15	++	14	+++
Hymenoptera														
Pseudopachylosticta subflavata (Cimbicidae)											3	++		
Bruchophagus sp. (Eurytomidae)					6	+++					5	+	3	+
Total number of sites surveyed	6		1		19		2		2		17		29	
Total number of herbivore species collected	2		1		9		2		3		12		6	

Note: The number of sites at which the species was found in each region and a measure of relative abundance is given for each species.
+ indicates that less than five individuals were sampled, ++ indicates that between 5 and 25 individuals were sampled and +++ indicates that over 25 individuals were sampled.

2.4. Mode of damage

The mode of damage inflicted by each insect species was observed in the field. Natural enemies that damaged the vascular tissue or mechanical support tissue of the plant were considered more promising potential biological control agents for *P. aculeata* than those that feed on the fruit, flowers, seeds or leaves.

2.5. Sampling effort

Species accumulation curves were constructed using EstimateS Version 7.5 (Colwell, 2005). The Chao 2 estimator was used to predict the number of natural enemy species associated with *P. aculeata*. This estimator is appropriate for estimating populations when abundances of species are unknown.

3. Results

3.1. Climatic matching and genotype matching

Climatic matching indicated that Rio de Janeiro Province, Santa Catarina Province and parts of Paraná Province in Brazil were the most suitable regions from which to collect potential biological control agents (Figure 4). Genotype matching indicated that the most closely related plants to the South African populations were found in Southern Brazil, with Rio de Janeiro Province being the closest match, followed by Santa Catarina Province (Paterson et al., 2009). Rio de Janeiro Province and Santa Catarina Province, Brazil, are therefore the most appropriate regions in which to collect biological control agents for release in South Africa.

A significant result from the climatic matching data was that Misiones Province in northern Argentina was considered a poor match to the South African climate (Figure 4). None of the six natural enemies found on *P. aculeata* were limited to Misiones Province despite the relatively high number of sites surveyed in that region (Table 3). The data indicate that Misiones Province should not be considered for further surveys. Genetic matching has also indicated that Rio de Janeiro and Santa Catarina provinces are better matches to the South African *P. aculeata* population than Misiones Province (Paterson et al., 2009).

Climatic matching also indicated that much of the northern region of the native distribution is less suitable for the collection of biological control agents (Figure 4). This region is also considered a poor region for collection of agents because the plants were genetically distinct from those in South Africa (Paterson et al., 2009). The northern region of the native distribution should thus not be considered for future surveys.

3.2. Distribution of insects associated with **Pereskia aculeata**

Seventy-seven *P. aculeata* sites in the native distribution were surveyed for natural enemies (Figure 3). Only 15 phytophagous natural enemy species were found associated with *P. aculeata* during all field surveys, including sampling at the eight long-term monitoring sites in Santa Catarina Province, Brazil (Table 3). Only two species, *Maracayia chlorisalis* (Walker) (Crambidae) and *Loxomorpha cambogialis* (Guenée) (Pyralidae) (formerly under the genus *Epipagis*), were recorded in the northern region of the native distribution and both of these species were also present in the southern native distribution.

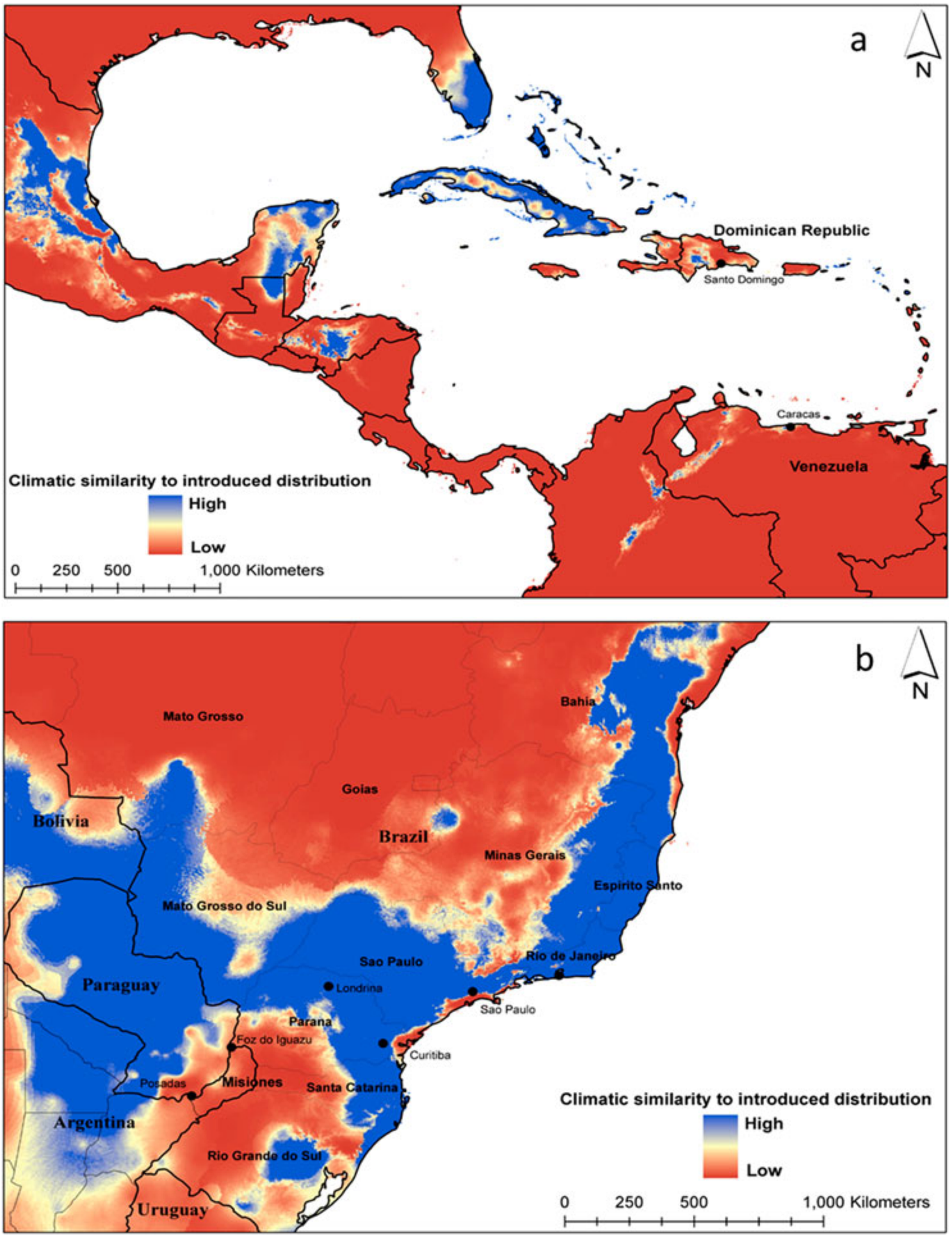

Figure 4. (Colour online) Climatic similarity to the introduced distribution of *P. aculeata* in South Africa in the southern (a) and northern (b) regions of the native distribution using Maxent (Philips et al., 2004, 2006).

Four species of Hemiptera, five Coleoptera, one Diptera, three Lepidoptera and two Hymenoptera were found associated with the plant (Table 3). No species were recorded in Misiones Province, Argentina, or in the northern region of the native distribution that were not recorded in other areas (Table 3). The region with the highest species richness was Santa Catarina Province where 12 species were recorded, 5 of which were only sampled in that region. Rio de Janeiro Province also had relatively high species richness with 10 species, 2 of which were only found in that region (Table 3). The high species richness found in Santa Catarina Province was not due to long-term monitoring in that region, but because only one new species (*Adetus analis* (Haldeman) (Cerambycidae)) was recorded at the long-term monitoring sites.

3.3. Field host range

Four species were eliminated as potential biological control agents due to previous host records. *Aetalion reticulatum* (Linné) (Aetalionidae) has a broad host range and has been recorded as a pest of *Eucalyptus cloeziana* (Myrtaceae) in South America (de Menezes et al., 2012; Ramoni-Perazzi, 2006). *Adetus analis* has been recorded as a pest of the Vegetable Pear or Chuchu (*Sechium edule* (Curcubitaceae)) which is grown as a minor crop in Brazil, Argentina and the USA. (De Souza Filho, Gabriel, & De Azevedo Filho, 2001). *Xyleborus affinis* Eichhoff (Scolytidae) has been recorded on *Pinus* species in Southern Brazil (Flechtmann, Ottati, & Berisford, 2001). Host specificity testing for *Loxomorpha cambogialis* (Guenée) (Pyralidae) has indicated that the host range of the insect includes species in closely related families to the Cactaceae, including the Portulacaceae and Bassellaceae, and was not considered adequately host-specific for release in South Africa (Klein, 1999).

No insects associated with *P. aculeata* were found feeding on *R. cereuscula* at the six sites where the two plant species co-occurred despite the stem-boring weevil *Cryptorhynchus* sp.(Curculionidae) being common on *P. aculeata* at all sites. When stems of the two plant species were dissected, *Cryptorhynchus* sp. Larvae were found at three of the six sites feeding on *P. aculeata* but not found in *R. cereuscula* plants. This suggests that *Cryptorhynchus* sp. may have a restricted host range making it a promising potential agent in terms of its field host range (Table 2).

During field host range observations, *Porphyrosela* sp. (Gracillariidae: Lithocolletinae) was observed feeding on *T. paniculatum* and *A. cordifolia,* suggesting a broad host range that would make it unsafe for release in South Africa (Table 2). *Pseudopachylosticta subflavata* (Kirby) (Cimbicidae) was observed developing on *T. paniculatum* in Paraná Province, Brazil, and is therefore not considered a priority for further research because it is likely that it could develop on *Talinum* species native to South Africa (Table 2).

3.4. Mode of damage

Membracis sp. (Membracidae), *Bolbonota* sp. (Membracidae) and *Bruchophagus* sp. (Eurytomidae) are not considered as promising potential agents due to the limited damage inflicted on the plant in the native distribution (Table 2). Damage inflicted by *Membracis* sp. is limited to tiny puncture marks in a spiral pattern with no associated necrosis of the leaf blade. *Bolbonota* sp. also produces tiny puncture marks without any other visible impact on the plant. *Bruchophagus* sp. produces a button gall of about 5 mm in diameter causing a slightly raised area on the surface of the leaf. Gall formation is rare or absent among *Bruchophagus* species and given recent changes in the delimitation of this genus (Lotfalizadeh, Delvare, & Rasplus, 2007); the generic placement of this species should be regarded as provisional. Even when *Bruchophagus* sp. is abundant the plants appear to be unaffected by the galling so the species is not considered suitably damaging for biological control (Paterson et al., 2011b). *Asphondylia* sp. (Cecidomyiidae) galls the ovaries of the flowers and stops the development of seeds in the fruit. This species could be effective at reducing the spread of *P. aculeata* to uninfested areas and so should be considered as a possible biological control agent if used in combination with more damaging agents (Table 2). The stem-wilting bug, *Catorhintha schaffneri* Brailovsky & Garcia (Coreidae), as well as the three stem-boring insects, *Cryptorhynchus* sp. (Curculionidae), *Acanthodoxus machacalis* Martins & Monné (Cerambycidae) and *Maracayia chlorisalis* (Walker) (Crambidae), are considered the promising potential agents in terms of their mode of damage (Table 2).

3.5. Sampling effort

The Chao 2 estimator (Colwell, 2005) predicted that all species associated with *P. aculeata* have been sampled and that no new species are expected if surveys were to continue (Figure 5). The upper 95% confidence limit of the Chao 2 estimator is 16.35 species after the 77 sites. This suggests that additional sampling will not significantly increase the number of species collected.

3.6. Promising potential biological control agents

Catorhintha schaffneri, *Acanthodoxus machacalis*, *Maracayia chlorisalis* and *Asphondylia* sp. were either suitable or unknown for all four criteria used for prioritisation and should therefore be considered priority species for further research (Table 2). *Cryptorhynchus* sp. is also considered promising despite not being found in Rio de Janeiro Province, Brazil, where the closest genetic matches to the South African

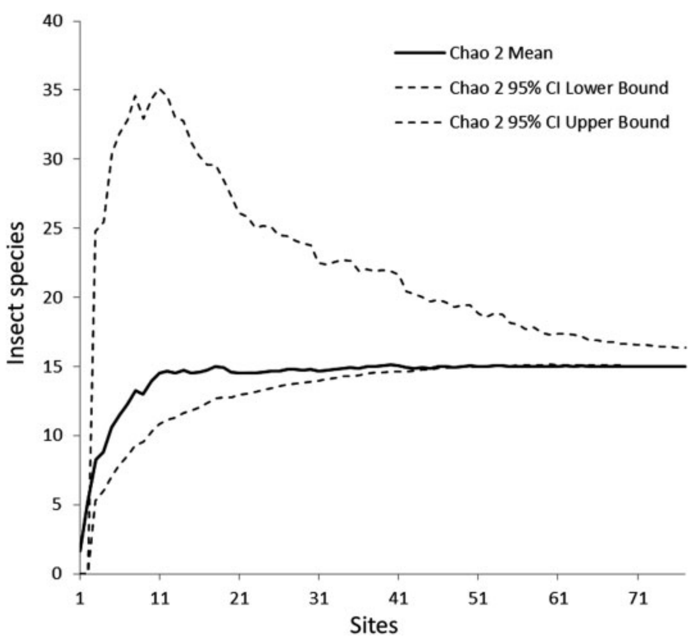

Figure 5. The Chao 2 estimator predicts (Colwell, 2005) that no new species will be encountered if further surveys are conducted.

P. aculeata population were found (Table 2). *Cryptorhynchus* sp. was restricted to Santa Catarina Province (Table 3) but was considered promising in terms of field host range, mode of damage and climatic matching (Table 2). *Pereskia aculeata* plants in Santa Catarina Province were genetically very similar to those in Rio de Janeiro and were the second closest match to plants found in South Africa (Paterson et al., 2009) so *Cryptorhynchus* sp. is likely to be compatible with the South African genotypes.

4. Discussion

The species richness of phytophagous insects associated with *P. aculeata* is low compared with species of *Lantana* (Verbenaceae) (Palmer & Pullen, 1995) and many other herbaceous plants (e.g. Fontes et al., 1994; Gillett et al., 1991; Harley et al., 1995), but is similar to other vine species such as *Lygodium microphyllum* (Cav.) R. Br. (Lygodiaceae) (Goolsby, Wrighe, & Pemberton, 2003), *Mikania micrantha* HBK (Compositaceae) (Cock, 1982), *Macfadyena unguis-cati* (L.) Gentry (Bignoniaceae) (Williams, Neser, & Madire, 2008) and *Cardiospermum gradiflorum* Sw. (Sapindaceae) (Simelane, Fourie, & Mawela, 2011). The low number of species associated with the plant is not a result of poor sampling effort as indicated by the species accumulation analysis. It is unlikely that further surveys would result in new natural enemy species being recorded, so biological control efforts should be focused on the species already known to be associated with the plant rather than on surveys for new potential agents.

The suite of insects associated with *P. aculeata* is unique compared with the faunal assemblages found associated with over 175 other Cactaceous species (Mann, 1969; Zimmermann, Erb, & McFadyen, 1979). The majority (75%) of cactophages recorded on other cactus species were internal feeders in the succulent cladodes (Zimmermann & Granata, 2002). Since species of *Pereskia* are atypical Cactaceae without succulent cladodes, a unique insect assemblage on *P. aculeata* was expected. With the exceptions of *L. cambogialis* and *M. chlorisalis*, which are known to feed on other Cactaceae (Mann, 1969; Zenner de Polania, 1990), none of the species recorded on *P. aculeata* are known from other cactus hosts. It is interesting that the only two species encountered in the northern region of the native distribution were generalist cactophages, because the lack of specialist herbivores suggests that the origin of *P. aculeata* may be in the southern region of the native distribution rather than in the north. It is possible that *P. aculeata* may have been introduced into the northern region of the presumed native distribution. *Pereskia aculeata* is often grown as a horticultural or food plant outside of its native range (Leuenberger, 1986). It is thus possible that *P. aculeata* was introduced into the northern region of the native distribution at such an early stage that it was considered native when the species was first described (Linnaeus, 1753). The only specimens used in the original description that had confirmed localities were cultivated plants from Jamaica (Leuenberger, 1986).

The most promising potential biological control agents, which should be the focus of further research including host specificity testing, are *Catorhintha schaffneri*, *Acanthodoxus machacalis, Cryptorhynchus* sp., *Maracayia chlorisalis* and *Asphondylia* sp. *Phenrica guerini*, the only biological control agent already released on *P. aculeata*, was considered promising in terms of host specificity as well as climatic and genetic matching but not in terms of its impact because feeding is usually restricted to the leaves. *Phenrica guerini* is not a particularly effective biological control agent in South Africa. Despite damage to the leaves of the plants at sites where *P. guerini* has become abundant, the density of *P. aculeata* was not visibly reduced (Paterson et al., 2011b).

Catorhintha schaffneri is a stem-wilting or stem-splitting bug that causes the young shoots of *P. aculeata* to die and rot. *Acanthodoxus machacalis* and *Cryptorhynchus* sp. are stem borers that damage the structural tissue of old stems and often destroy the vascular tissue causing the plant to die above the mine. *Maracayia chlorisalis* mines the young shoots usually causing the damaged shoot to die. *Asphondylia* sp. galls the ovaries of the flowers and stops the development of seeds. Although *P. aculeata* propagates primarily through vegetative reproduction, the dispersal of seeds after birds or bats have eaten the fruit is likely to be important in the invasion of new sites, especially, in protected and remote areas. Reducing the seed set of the plant in South Africa could therefore reduce the spread of the weed. A combination of a shoot-attacking insect, such as *C. schaffneri* or *M. chlorisalis*, and a stem-attacking insect, such as *Cryptorhynchus* sp. Or *Acanthodoxus machacalis*, is likely to be a damaging combination and would reduce competition between biological control agent species for the same resource. The seed-attacking species, *Asphondylia* sp., could be released in combination with any of the other promising potential agents.

All of the most promising potential agents could be useful for the control of *P. aculeata* in South Africa and all should be considered for host specificity testing. Host records only exist for *M. chlorislais* which has been recorded feeding on two Cactaceous species, *Hylocereus undata* Britton & Rose (CESAVEP, 2006) and *Hylocereus ocamponis* (Salm-Dyck) Britton & Rose (Zenner de Polania, 1990), but never on any species outside of the family Cactaceae. Only one species of Cactaceae, *Rhipsalis baccifera*, is considered native in South Africa (Dyer, 1975; Germishuizen & Meyer, 2003) so species with host ranges limited to the Cactaceae could still be suitable for release.

In this study, climatic matching and genotype matching were useful for prioritisation of regions in the native distribution in which to focus surveys. Fortunately, close genetic matches to the South African *P. aculeata* population were found within regions that were climatically suitable and that had high diversities of insect species compared to other regions. Field host range data and observations of impact on the plant in the native distribution could then be used to exclude species that were unlikely to be suitably host-specific or damaging. By selecting the most promising of the potential biological control agents for further study, the risk of conducting host specificity studies on unsuitable natural enemies is reduced, resulting in more efficient use of the biological control researcher's time and resources.

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