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Environmental factors influencing the distribution of *Opuntia stricta*, an invasive alien plant in the Kruger National Park, South Africa

L.C. Foxcroft [a,b,*], J.H. Hoffmann [c], J.J. Viljoen [a], J.J. Kotze [a]

[a] *Tshwane University of Technology, Department of Nature Conservation, Private Bag X680, Pretoria 0001, South Africa*
[b] *Savanna Ecological Research Unit, Private Bag X402, Skukuza 1350, South Africa*
[c] *Zoology Department, University of Cape Town, Rondebosch 7700, South Africa*

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Abstract

Opuntia stricta (Cactaceae), an alien weed, has invaded an area of more than 35 000 ha in the Skukuza region of the Kruger National Park [KNP]. The distribution of the plant and features of the environment were used to identify biotic and abiotic factors which may be affecting the distribution and density of the plant. A Canonical Community Analysis revealed that none of the environmental factors that were monitored influenced the distribution or abundance of *O. stricta* in KNP. There were no apparent natural barriers that might limit the occurrence of *O. stricta* within the KNP. The study provides insight into the relationship between the invader and host environment, showing that there is a high probability that, unless there is appropriate intervention, *O. stricta* will eventually colonise the entire KNP.

Keywords: Alien invader; *Cactoblastis cactorum*; Canonical Community Analysis; Environmental correlates; Weed

1. Introduction

One of the greatest threats to the conservation status of the Kruger National Park [KNP], South Africa, is an invasive cactus species, *Opuntia stricta* (Haworth) Haworth. Over the past 50 years *O. stricta* has spread into an area of more than 35 000 ha within the KNP, forming impenetrable thickets which smother indigenous vegetation and restrict movement and forage of animals (Lotter and Hoffmann, 1998).

As with other plant taxa, the distribution patterns of cacti in their native ranges are influenced by a range of environmental factors (Montana, 1990). For example, the local distribution of many cacti is governed by the texture of soil and degree of slope, both of which affect drainage (Anthony, 1954). However when introduced into a new region, some plant species thrive, out-competing indigenous species and exhibiting an ability to overcome environmental constraints, and in the process overrunning the invaded area (Keane and Crawley, 2002).

Over the years, KNP management has used a combination of integrated control methods, including chemical, mechanical and biological, in attempts to bring the *O. stricta* invasion under control, with varying degrees of success (Lotter and Hoffmann, 1998). The biological control campaign relied initially on the cactus moth, *Cactoblastis cactorum* (Lepidotera: Pyralidae) (Hoffmann et al., 1998a,b), which had been so successful against *O. stricta* in Australia in the 1930s (Dodd, 1940). More recently a cochineal insect, *Dactylopius opuntiae* (Homoptera: Dactylopiidae) has also played a major role in managing the weed (Hoffmann et al., 1999; Volchansky et al., 1999; Foxcroft and Hoffmann, 2000). In order to prioritise control efforts there was a need to identify areas at greatest risk of invasion, as opposed to areas where invasion is unlikely. This study was initiated to determine the biotic and abiotic factors that influence the reproduction and survival of *O. stricta* and thereby gather information that would allow us to delineate areas where the weed is most, and least, likely to invade and form dense thickets.

2. Materials and methods

2.1. Data collection

The project was conducted around Skukuza, in the southern region of the KNP, that has been invaded by *O. stricta* (Lotter and

* Corresponding author. Tel.: +27 13 735 4125; fax: +27 13 735 4055.
E-mail address: llewellynf@sanparks.org (L.C. Foxcroft).

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Table 1
Variables used to characterise *Opuntia stricta* distribution in the Kruger National Park

Variables	Categories
GPS co-ordinates	Recorded in degrees decimal
Plant size − plants < 459 cladodes	Direct count of number of cladodes
Plant size − plants > 459 cladodes	Measurement of Length × Breadth × Height was taken for extrapolation by the following regression: $\text{Log}N=\log V^{0.515}+2.575$, where N is the number of cladodes on the plant and V is the volume of the plant (approximating a cap) and calculated from the following equation: $V=\pi H/24(H2+12(L+B)/4)^2/2$, where H is the height, L is the length, and B is the breadth of the plant, as described by Hoffmann et al. (1998a). Plant records were then divided into seven size class categories, namely: 1–10, 11–35, 36–79, 80–146, 147–229, 230–400 and 401–2788 cladodes
C. cactorum presence or absence	Any sign of *C. cactorum* damage on a plant, egg sticks or remnants thereof or actual insects visible was recorded as present in order to overcome any seasonal variability
Substrate	Soil, stony soil, bare rock, boulders, pebbles, mud, termite mound, trunk, branch
Vegetation type	Vlei grassland, dry grassland, open shrubland, closed shrubland, savanna, open woodland, closed woodland, riverine thicket, riverine forest, forest
Water regime	Koppie (small hillock), boulder outcrop, rainwater in rock hollow, dryland (veld), levee, floodplain, dry riverbed, seasonal river, perennial river, stagnant river pool, seasonal vlei (wetland), perennial vlei, seasonal isolated 'pan', perennial isolated 'pan', pan on drainage line, seepage area, cold spring, hot spring, dam, drinking trough
Distance to nearest *O. stricta* plant (if single) or to centre of nearest clump	1–6.9; 7–12.9; 13–19.9; 20–28.9; 29–39.9; 40–52.9; 53–70.9; 71–96.9; 97–131.9; 132–175.9; 176–237.9; 238–328.9; 329–615.9; 616–1103.9; 1104–2486 m
Roads	Tar roads, gravel roads, management roads. An impact zone (buffer) of 30, 20 and 5 m respectively, was added along the edges of the roads so as to determine the zone of potential impact from the roadside on *O. stricta*
Rivers	Main (example, Sabie River), secondary (example, N'waswitshaka River) and tertiary (other streams). The buffer (impact) zones were as follows: 200, 50 and 20 m respectively
Fire return frequency	Number of times an area was burned during the last 45 years (period for which sufficient data was available)
Past management history of *O. stricta*	Expressed as the number of years that each individual *Opuntia* management unit was sprayed in the last nine years (period for which a planned and routine spray programme was carried out)
Soil form (SCWG, 1991)	Hutton, Avalon, Clovelly, Glencoe, Westleigh, Lithosols, Valsrivier, Cartref, Estcourt, Glenrosa, Swartland, Shortlands, Bonheim, Mayo, Arcadia, Rensburg
Soil depth	Very deep, deep, medium deep, medium shallow, shallow, very shallow and water bodies
Soil clay content (soil texture)	Very sandy, sandy, loamy sand, sandy loam, loam, loam and clay, clayey, clay, water bodies
Dominant woody vegetation type (Kemp et al., 1997)	Expressed as areas dominated by broad-leaved *Combretum–Terminalia* or *Colophospermum mopane* woodland, by fine-leaved *Acacia–Albizia–Dichrostachys* woodland, by mixed woodland, by riparian woodland or by open areas lacking woody vegetation
Percentage open areas (Kemp et al., 1997)	Expressed as present, occasional, frequent or extensive
Grass cover (Kemp et al., 1997)	Presented as present (0–25%), occasional (26–50%), frequent (51–75%) or extensive (76–100%)

Hoffmann, 1998). Field variables were collected from November 2000 to April 2002 (Table 1). The entire area was systematically searched, mostly during routine control operations, and the positions of all plants or clusters of plants that were encountered were recorded by means of a GPS receiver [Geographic Positioning System] (Garmin 12XL; horizontal accuracy 7–15 m), totalling approximately 5000 records. Besides position, the size of the plants (see Table 2) and whether they had *C. cactorum* damage were recorded. Additional variables (environmental features) were extracted from GIS (Geographic Information System) layers maintained in the KNP GIS lab and analysed with Arcview (version 3.2a) GIS software.

2.2. Statistical processing

Canonical Community Analysis [CCA], (as provided in CANOCO; Ter Braak, 1998) was carried out to establish patterns and associations between *O. stricta* and the environment and the potential impacts thereof. Species and environment data were used to extract patterns from the explained variation (direct gradient analysis). The forward selection summary (in CANOCO) was also used, as this feature is useful for ranking environmental variables in importance, thereby reducing a large set of environmental variables. The variables were selected automatically, where the K best variables were selected sequentially on the basis of maximum extra fit. Thereafter, the statistical significance of each selected variable was judged by a Monte Carlo permutation test. Monte Carlo permutation tests are

Table 2
Monte Carlo significance test (499 permutations under the reduced model). Eigen values are given between 0–1 and explain the % variance accounted for by that axis

Axes	1	2	3	4	Total inertia
Eigen values	0.325	0.034	0.032	0.016	0.420
Species–environment correlations	1.000	1.000	1.000	1.000	
Cumulative percentage variance-					
of species data:	77.4	85.5	93.1	97.0	
of species–environment relation:	77.4	85.5	93.1	97.0	
Sum of all unconstrained Eigen values:					0.420
Sum of all canonical Eigen values:					0.420

Summary of Monte Carlo significance test

Test of significance of first canonical axis:	Eigen value = 0.325 F-ratio = 0.000 p-value = 1.0000
Test of significance of all canonical axes:	Trace = 0.420 F-ratio = 0.000 p-value = 1.0000

frequently used to select a subset of variables that explain the species data nearly as well as the full data set for the construction of the CCA biplot (ordination diagram).

Analysis of variance (ANOVA, as provided in STATISTICA) was computed to determine whether the differences in *O. stricta* density classes, as suggested by the ordination diagrams, were in fact discrete categories. Tukey's HSD unequal *n* (Spjotvoll/Stoline) test was used to determine variance at $p<0.05$ (95%).

3. Results

The CCA and ordination diagram (Fig. 1) clumped *O. stricta* density into five main groups, namely, very high (dist 1), high (dist 2), medium (dist 3–7), low (dist 8–12) and very low (dist 13–15). The first axis accounts for 77.4% of the observed variation (Eigen value = 0.325) (Table 2).

The forward selection summary (Table 3), indicates that large plants (230–400 cladodes, size 6; $p=0.026$, Lambda = 0.19), fine-leaved woodlands (*Acacia* bush — domwd1; $p=0.002$, Lambda = 0.13), open shrubland (h2; $p=0.018$, Lambda = 0.04) and *C. cactorum* absence (Cact abs; $p=0.008$, Lambda = 0.02) describe the largest variation in the ordination diagram.

To validate the pattern indicated for *O. stricta* density, ANOVA was computed to determine whether the suggested density classes differed from each other significantly and offer a useful classification. All the classes differed from each other significantly where, at "very high" and "high" density classes, $p<0.043$, and for all other classes, $p<0.001$ (Fig. 2). Therefore

Table 3
Forward Selection (FS) summary of data analysed that may potentially impact on *O. stricta* presence or absence

Variable	Conditional effects			
	Var. *N*	Lambda	*p*	*F*
O. stricta plant size: 230–400 cladodes (size 6)	21	0.19	0.026	5.94
Fine-leaved (*Acacia*) woodland (domwd1)	7	0.13	0.002	7.03
Nine herbicidal control operations (spray9)	30	0.03	0.142	2.58
Open shrubland (h2)	13	0.04	0.018	4.81
Absence of *C. cactorum* (Cact abs)	3	0.02	0.008	6.04
Grass cover 51–75% (grass1)	12	0	0.25	1.91
Extensive occurrence of bare ground patches (BG1)	1	0.01	0.556	0.93
Occasional occurrence of bare ground patches (BG3)	2	0	1	0

Var. *N* indicates the variable number; Lambda values provide a test of significance for the squared canonical correlation; *p*-values are based on 499 Monte Carlo permutations under the reduced model; The *F* statistic represents a test of the null hypothesis that the expected values of the regression coefficients are equal to each other and that they equal zero.

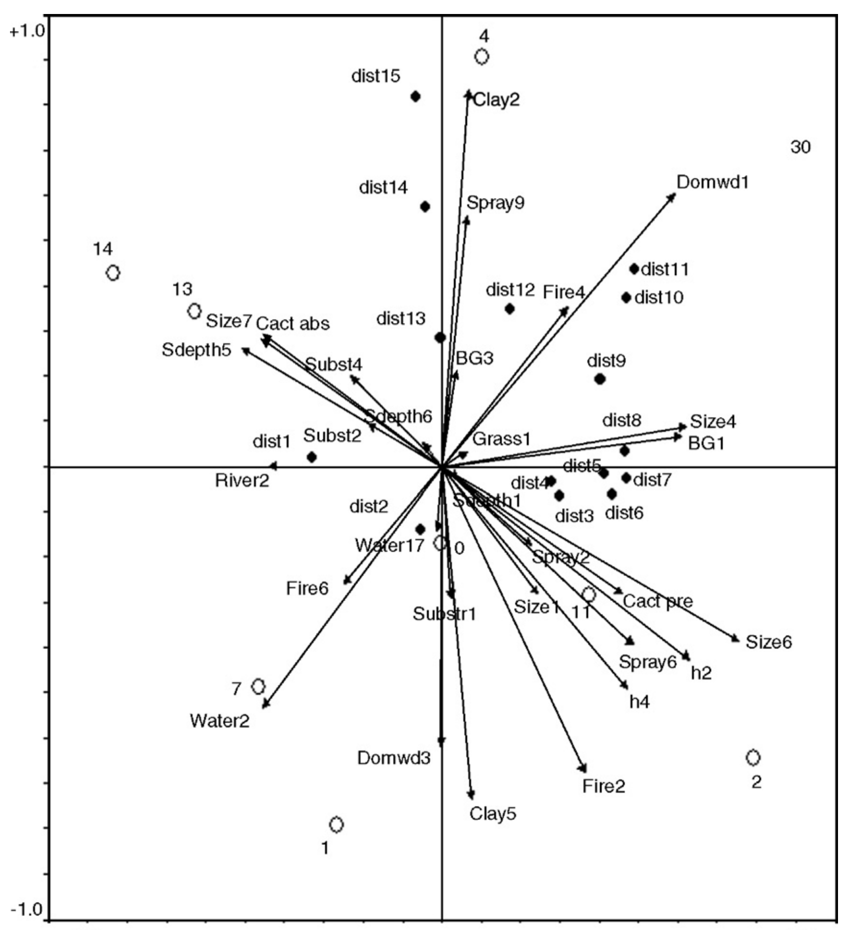

Fig. 1. Canonical Community Analysis (CCA) diagram (scaling: Interspecies distance; Standardisation by Species-centred and Standardisation by Samples-centred), which indicates the impact of the environmental variables on *O. stricta* density. [(○) sample plots, (♦) relative density of *O. stricta*].

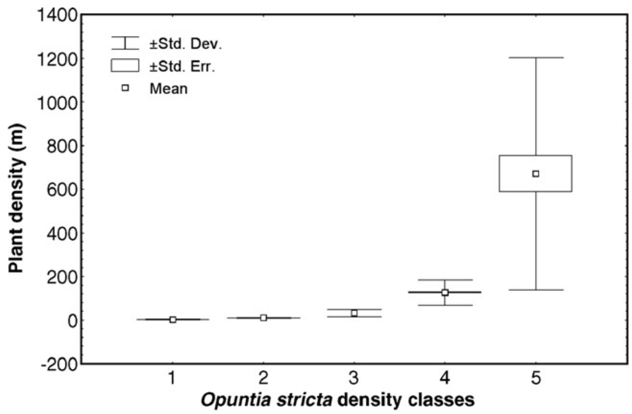

Fig. 2. Box and whisker plot of *O. stricta* density classes. Plant density is calculated as relative density or mean distance to nearest neighbour.

the following *O. stricta* density classes were used: very high (plants 1–6.9 m apart), high (plants 7–12.9 m apart), medium (plants 13–70.9 m apart), low (plants 71–328.9 m apart) and very low (plants 329–2486 m apart) (Fig. 2).

In general the plants exhibited a tendency towards a densely clumped distribution. This can be determined by the variance ($n\Sigma x^2-(\Sigma)^2/n(n-1)$) of *O. stricta* density, relative to the mean ($\Sigma x/n$), where the variance is greater than the mean, distribution is clumped. The degree to which the variance is greater than the mean, provides an indication of the degree to which the plants exhibit clumped distribution (Kershaw, 1973). In the KNP, the ratio was 236:1, (mean = 0.4% of the variance) indicating a highly clumped distribution of *O. stricta*.

4. Discussion

No clear patterns or variables emerged to satisfactorily explain the *O. stricta* distribution patterns. This was however not unexpected, as plants have been observed growing in unlikely positions such as in rock crevices, on tree forks and even on corrugated iron sheets (L.C. Foxcroft, pers. obs.). In a similar study using different methods and examining the role of propagule pressure in structuring invading populations, Foxcroft et al. (2004) also found no environmental correlates.

Although the results of the forward selection summary suggest that fine-leaved (*Acacia*) woodlands and open shrubland were important, the results do not provide a convincing basis for this argument.

Results from the CCA indicated that although certain associations between factors are revealed, they were in most cases tenuous. There was also no specific, single factor that was more significant than the others. As a result, it was not possible to describe specific environmental factors that were influential in determining or predicting *O. stricta* density. Therefore, the results suggest that *O. stricta* is tolerant of a wide range of ecological conditions and all of the regions of the KNP need to be considered equally when management plans are being formulated. This also correlates to the distribution of *O. stricta* at a larger spatial scale, where Henderson (2001) indicates this species to be found widely across South Africa. This also serves as a further indication of the change in relationship between plant and environment observed, when a species is introduced into a new environment and where it is freed from its natural enemies.

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