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Landscape degradation may contribute to large-scale die-offs of *Euphorbia ingens* in South Africa

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ABSTRACT

Euphorbia ingens, a large succulent tree species native to southern African savanna ecosystems, has died in large numbers in recent years in some areas of South Africa. A previous study found that changes in climate (higher temperatures and lower or more variable rainfall) likely play an important role in causing mortality. However, anecdotal evidence suggests that stress due to habitat degradation may also contribute to *E. ingens* die-offs. In this study, we evaluated *E. ingens* die-offs in South Africa at 10 sites. Specifically, we aimed to examine the roles of both climate and landscape degradation in causing the die-offs. We used a combination of climate data, estimates of tree mortality and ratings of die-off symptoms (categories of grey discoloration and rotting associated with moth attacks), and proxies for landscape degradation associated with livestock grazing. We assessed which sites exhibited greater mortality and die-off associated symptoms, and whether they exhibited spatial auto-correlation (did distance between sites correlate with severity of *E. ingens* die-off?). We also used correlation analysis to compare tree mortality to proxies of savanna ecosystem degradation. These proxies were dung counts (livestock), woody debris counts, plant and bare soil cover, soil nutrients, and density of *Dichrostachys cinerea* (Fabaceae), a savanna plant that dominates when disturbance is high. Minimum and maximum temperatures as well as precipitation were compared among sites. There was no spatial auto-correlation between distance and die-off severity among sites, and sites with greater levels of tree mortality were associated with proxies indicating degradation. This suggests that die-offs of *E. ingens* are likely due to a complex of stressors, including both changes in climate and poor land-use practices. Our results indicate that sustainable rangeland practising of South African savannas may aid in conserving *E. ingens* and retaining this iconic tree on the landscape.

1. Introduction

Euphorbia ingens E. Meyer: Boissier is native to southern Africa where it is found primarily in savanna ecosystems (Van Wyk and Van Wyk, 1997; Palgrave et al., 2002). It is a large succulent tree with a branching crown and a main woody stem supported by a shallow, widely-spread root system (Van Wyk and Van Wyk, 1997; Palgrave et al., 2002; Gildenhuys, 2006). Several animals rely on this tree for moisture and nutrients (most notably nitrogen), especially during periods of drought (Dudley, 1997; Brown et al., 2003; Heilmann et al., 2006). Culturally, the tree is important to local human communities that use the chemically complex latex it produces to stun or kill fish allowing easy capture and to produce an array of traditional medicines (Dudley, 1997; Brown et al., 2003; Gildenhuys, 2006; Heilmann et al., 2006). The tree is also one of the most iconic examples of convergent evolution in the world (Bennici, 2002; Horn et al., 2012).

Unfortunately, rapid localized die-offs of *E. ingens* are increasingly reported. The first reports of high levels of mortality of the tree were from the Limpopo Province of South Africa (Malan, 2006; Roux et al., 2008, 2009). The main symptoms exhibited by dying trees were a gray discoloration of the succulent branches and the rotting of branches associated with feeding by the larvae of a moth in the genus *Megasis* Guenée (Lepidoptera: Pyralidae) (Malan, 2006; Roux et al., 2008, 2009; Van der Linde et al., 2011a). Subsequent studies revealed that various beetles and fungi were associated with diseased and dying *E. ingens*, but none were clear primary causal agents of mortality (Van der Linde et al., 2011b, 2011c, 2016).

Van der Linde et al. (2012) found evidence that changes in climatic conditions (higher temperatures and lower or more variable rainfall) were involved in *E. ingens* die-offs. Changes in local climate could result in stress to *E. ingens*, allowing insects and pathogens, that are otherwise relatively benign, to contribute to tree mortality. However, anecdotal

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observations also suggested that die-offs may be triggered by locally-induced stressors such as poor land-use practices, including intensive grazing. However, the hypothesis that land degradation plays a role had not been investigated.

The savanna ecosystem in which *E. ingens* occurs covers approximately 35% of South Africa (Scholes, 1997; Scholes and Archer, 1997). Savanna ecosystems are maintained by interactions among fire, herbivory and precipitation (Backéus, 1992; Scholes, 1997; Scholes and Archer, 1997; Van Langevelde et al., 2003; Archibald et al., 2005; Van Wilgen, 2009). Two types of savanna systems occur in South Africa; mesic savanna and xeric savanna which are differentiated by mean annual precipitation (Scholes, 1997). Mesic savanna landscapes generally have a higher woody component compared to xeric savannas due to higher rainfall (Scholes, 1997; Scholes and Archer, 1997). Xeric savannas are drier with a lower woody plant to grass ratio (Scholes, 1997). Historic fire regimes maintain both grasses and trees in savannas (Bond et al., 2003). A lack of fire or reduction in mean fire intervals, due to fire suppression, can lead to increased woody vegetation and a loss of grass cover especially in mesic savanna (Bond et al., 2003; Sankaran et al., 2005; Van Wilgen et al., 2008; Van Wilgen, 2009; Parr et al., 2012). In contrast, higher mean fire return intervals due to human-caused fires lead to reduced woody and grass cover in mesic and xeric savannas respectively (Bond et al., 2003; Van Wilgen, 2009; Parr et al., 2012). Herbivory also plays an important role in maintaining the ratio of grass to woody plants typical of savannas (Scholes and Archer, 1997; Van Langevelde et al., 2003; Wakeling and Bond, 2007). In particular, grazers are most important in xeric savannas while browsers are more important in mesic savannas (Scholes and Archer, 1997; Van Langevelde et al., 2003; Wakeling and Bond, 2007).

Apart from the direct effect on grass to tree ratios, herbivores indirectly affect savanna ecosystems by their physical activities. In the context of human land use effects, livestock can have major negative effects on plant communities through high levels of grazing, trampling, and compaction (Scholes and Archer, 1997; Van Langevelde et al., 2003). Overgrazing, especially in environments with clay soils, can lead to soil degradation, soil compaction (reducing water infiltration and thus water availability), higher surface run-off (that can wash away important water soluble nutrients needed by plants, e.g. nitrate) and crust formation. All of these can reduce the ability of grasses and trees to grow (Kelly and Walker, 1976; Rietkerk et al., 1997, 2000; Van Langevelde et al., 2003; Savadogo et al., 2007).

Savanna ecosystems in South Africa are under increasing pressure to support livestock production (Scholes, 1997; Wakeling and Bond, 2007; Van Wilgen, 2009). Overstocking is common and fire suppression is often practiced to protect the animals (Van Langevelde et al., 2003; Van Wilgen, 2009). Overgrazing and fire suppression in savanna ecosystems not only leads to a loss of grass cover and erosion (Scholes, 1997; Bond et al., 2003; Van Langevelde et al., 2003), but also encroachment by woody pioneer species (Roques et al., 2001; Wakeling and Bond, 2007).

In South Africa, *Dichrostachys cinerea* Wight and Arn., a native woody plant, is a common encroacher in response to overgrazing (Hoffman et al., 1999; Roques et al., 2001; Wakeling and Bond, 2007; Orwa et al., 2009). Herbivores feed on the seed capsules of the plant and play a major role in its dispersal, while locally the plant can spread as a clone through lateral roots (Hoffman et al., 1999; Wakeling and Bond, 2007). This allows *D. cinerea* to establish very quickly in a poorly managed system such as one with high levels of grazing, a high percentage bare soil and reduced fires. Once established, it becomes very difficult to control (Wakeling and Bond, 2007).

The overall objective of this study was to elucidate the factors leading to the massive rapid die-offs of *E. ingens* in South Africa. We revisited sites previously studied by Van der Linde et al. (2012) and included a number of new sites to increase sampling frequency and geographic distribution. The specific objectives were to 1) re-examine the role that climate plays in current patterns of *E. ingens* die-off and 2) investigate whether tree mortality could also be associated with factors related to landscape degradation.

2. Materials and methods

2.1. Study sites

Study sites included five previously sampled by Van der Linde et al. (2012) in 2010, as well as five new sites. Of the previously sampled sites, three were located in the Limpopo Province [Euphorbia Drive (coordinates: 24°10′14.02″S 29°3′4.86″E, elevation: 1180 m), Last Post (23°17′21.39″S 29°55′27.93″E, 940 m) and Capricorn (23°21′50.67″S 29°44′40.27″E, 1110 m)], and two in the North West Province [Enzelsberg (25°22′58.05″S 26°16′4.21″E, 1170 m) and Wolfaan (25°42′59.27″S 27°42′9.24″E, 1236 m)] of South Africa. Of the new sites, two were located in the province of KwaZulu Natal [Eshowe (28°48′42.64″S 31°30′30.10″E, 450 m) and Ulundi (28°26′8.47″S 31°18′25.70″E, 735 m)], two in Limpopo [Bela-Bela (24°51′48.30″S 28°20′5.90″E, 1200 m) and Modimolle (24°44′53.75″S 28°21′55.43″E, 1216 m)] and one in Mpumalanga [Lydenburg (24°55′53.87″S 30°19′7.09″E, 1155 m)] (Fig. 1). The sites were chosen from accessible *E. ingens* populations, where we had permission to conduct field studies, from each province in South Africa where this tree occurs.

2.2. Assessment of *E. ingens* mortality, degree of die-off, and the relationship of mortality and symptoms to climate and landscape variables

At each site, eight 100 m × 50 m transects were established. Measurements were conducted in November 2014, coinciding with the timeframes used for previous sampling in 2010 and 2012. Within each transect, symptoms associated with die-off (gray discoloration and rotting associated with *Megasis* sp., hereafter referred to as moth damage) were scored for each living tree within each transect (mature and juveniles). Dead trees were also counted and percentage mortality was calculated relative to total trees in each transect. The age class of trees was not evaluated in this study as it was previously shown that both young and old trees are equally affected and that mortality is not related to age (Van der Linde et al., 2012).

Gray discoloration and moth damage were scored, independently of one another, based on a ranking system of zero to four [1: (1–25% succulent branches gray discolored and rotten from moth damage), 2: (26–50%), 3: (51–75%), 4: (76–100%)]. Gray discoloration and moth damage have different patterns of disease progress on *E. ingens* trees, hence they were scored using different systems. Gray discoloration starts at the bottom end of the tree just above the trunk and gradually moves upwards to the crown while moth damage generally affects the succulent branches more or less randomly (Figs. 2 and 3). Not all sites were monitored for the same period of time, therefore, percentage mortality and estimations of disease severity were compared using data from a four-year period for Enzelsberg, Wolfaan, Euphorbia Drive, Capricorn and Last Post (2010–2014) and a two-year period for Bela-Bela, Modimolle, Lydenburg, Ulundi and Eshowe (2012–2014).

To score environmental variables (proxies) associated with savanna degradation, a linear 100 m belt transect was established within each of the 100 m × 50 m transects at each site. Quadrants (1 × 1 m) were located every 2 m within each transect (50 quadrants × 8 transects per site = 400 quadrants per site). Within each quadrant, the percentage area covered by living plants and bare soil was estimated. Coverage of dung and dead wood within each quadrant was estimated using a ranking system of low (wood or dung clumps did not occur or only occurred in one quarter of the quadrant), medium (wood or dung clumps occurred in half of the quadrant area) and high (wood or dung clumps occurred in three quarters of the quadrant area). This classification was used rather than percentage cover because these variables

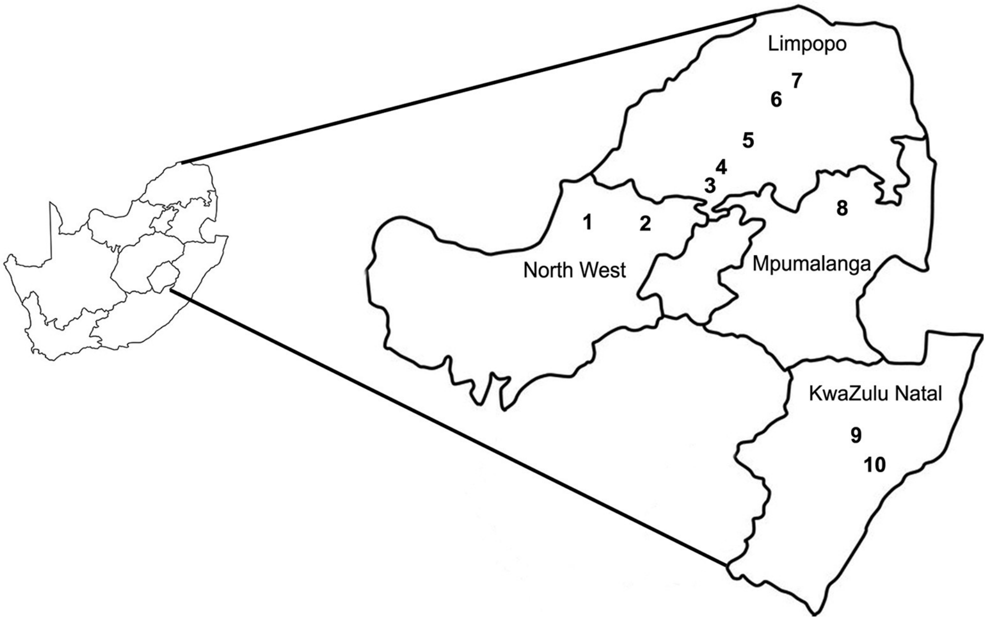

Fig. 1. Sites at which *Euphorbia ingens* die-offs were investigated. 1 = Enzelsberg, 2 = Wolfaan, 3 = Bela-Bela, 4 = Modimolle, 5 = Euphorbia Drive, 6 = Capricorn, 7 = Last Post, 8 = Lydenburg, 9 = Ulundi and 10 = Eshowe.

often consisted of scattered fecal pellets, which made a discrete estimate of percentage cover difficult.

Dichrostachys cinerea encroachment within each transect at each site was scored based on a binary rank (low or high). *Dichrostachys cinerea* was scored around each *E. ingens* tree within a transect, with low being less than 50% of around each *E. ingens* tree surrounded by *D. cinerea* and high being more than 50% of the *E. ingens* tree encroached by *D. cinerea*. The area scored around each *E. ingens* tree for *D. cinerea* encroachment was determined using the crown size of the *E. ingens* tree in question. This binary system used to score *D. cinerea* was deemed more appropriate than using the quadrant data since *D. cinerea* trees typically occurred around *E. ingens* individuals and in most cases there were either very dense stands of *D. cinerea*, or hardly any plants present.

For soil analyses, the first 954 cm^3 (at a depth of 15 cm) of top soil was taken every 20 m on each 100 m belt transect. Since we only wished to compare sites (and not individual transects within a site), soil

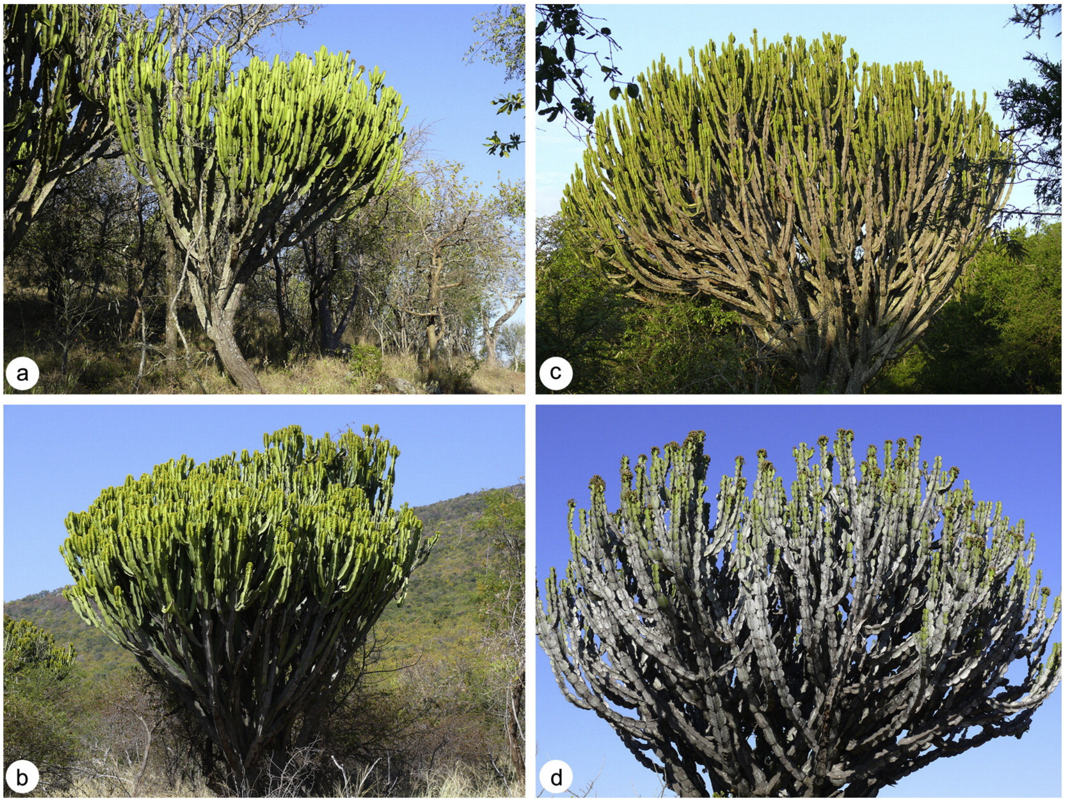

Fig. 2. Ranking of gray discoloration on *Euphorbia ingens* trees. (a) G1 (0–25% affected). (b) G2 (26–50% affected). (c) G3 (51–75% affected). (d) G4 (76–100% affected).

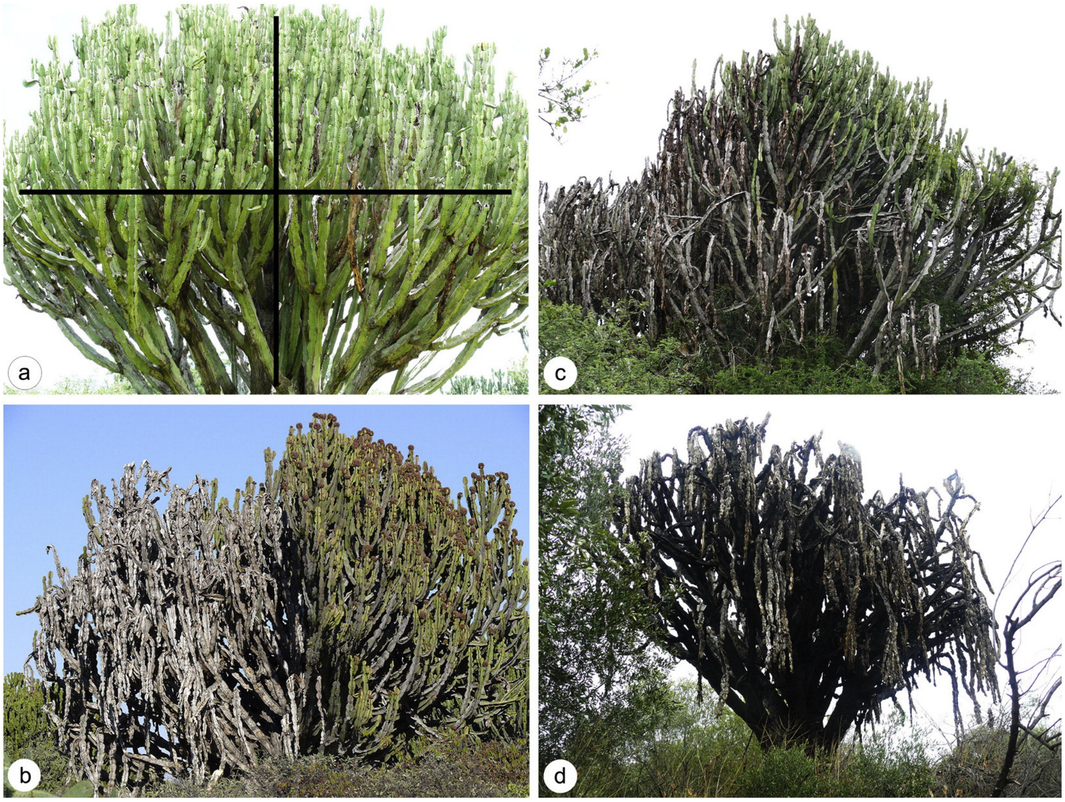

Fig. 3. Ranking of rotting associated with *Megasis* attacks on *Euphorbia ingens*. The crown of an *Euphorbia ingens* tree is divided into four quadrants and the percentage damage was calculated according to the proportion of quadrants containing moth-damaged branches. (a) M1 (0–25% affected). (b) M2 (26–50% affected). (c) M3 (51–75% affected). (d) M4 (76–100% affected).

samples from all eight transects within a site were pooled. Samples were transported to the laboratory and dried. Rocks, twigs and insects, were removed before analyses. Soil samples were analyzed by the Department of Plant Production and Soil Science, at the University of Pretoria, for texture, pH, percent carbon, mineral nitrogen, phosphorus and cation exchange capacity (CEC). The soil pH was determined using a 1:2.5 soil water ratio suspension (Schofield and Taylor, 1955), CEC was determined using a pH drop with ammonium acetate (1 M dm^{-3}) solution buffered at pH 7 (Schollenberger and Simon, 1945) with the hydrometer method used to determine particle size (Bouyoucos, 1962). Organic carbon content was determined using the Walkley-Black method (Walkley, 1935), ammonium and nitrate were extracted with 2 M potassium chloride using a 1:10 soil:extractant ratio and a 1 hour end-over-end shake followed by filtration (Magill and Aber, 2000; Shahandeh et al., 2005) while phosphorus was determined by the extraction method of Bray and Kurtz (1945).

Precipitation and temperature data for each site were obtained from the South African Weather Service (www.weathersa.co.za). Weather stations used were Lydenburg (station code: 0554816A7, distance from site: 27.8 km) for the Lydenburg site, Warmbad Towoomba (05895941, 4 km and 17 km) for Bela-Bela and Modimolle, and Babanango (03373825, 11 km) for Ulundi and Mtunzini (03043576, 25 km) for Eshowe. The same weather stations that were used by Van der Linde et al. (2012) for Enzelsberg (Tuscany, distance from site: 16 km [precipitation] and Marico, 17 km [temperature]), Wolfaan (Brits Hartbeespoortdam, 19 km [precipitation] and Buffelspoort II AGR, 18 km [temperature]), Euphorbia Drive (Palmer estate, 6 km [precipitation] and Mokopane, 18 km [temperature]), Capricorn (Mara-Pol, 30 km [precipitation] and Mara, 49 km [temperature]) and Last Post (Mara, 40 km [precipitation and temperature]) were used. Daily (minimum and maximum) temperatures and precipitation data were used to calculate monthly means and these were compared to determine if there were any changes over time that might account for increased mortality. Precipitation and temperature data were available for all but three sites from 1960 to 2014. The exceptions were Euphorbia Drive, Eshowe and Ulundi for which data were available only from 1996 to 2014.

2.3. Data analyses

Analysis of variance (ANOVA) was used to determine if there were significant differences in die-off symptoms (moth damage and gray discoloration) and mortality among sites. ANOVA was conducted using the mean percentage values of mortality and mean rank of the proportion of trees with gray discoloration or moth damage (from data acquired in 2014) in each transect for each site. In order to determine if there were changes in symptom severity and mortality over time; data from 2010 (Van der Linde et al., 2012) and 2012 were compared with data acquired in 2014. The mean rank of each die-off symptom (gray discoloration and

Table 1
Mean (SE) die-off factor and percentage mortality of *Euphorbia ingens* among all sites investigated in 2014.

Site	Gray discoloration	Moth damage	% mortality
Bela-Bela	0.560 (0.071)^{bcd}	0.504 (0.092)^{ab}	14.90 (2.04)^{bcd}
Capricorn	0.739 (0.082)^{b}	0.170 (0.026)^{cd}	2.50 (1.73)^{d}
Euphorbia Drive	1.695 (0.073)^{a}	0.597 (0.055)^{ab}	25.50 (5.10)^{ab}
Enzelsberg	0.148 (0.056)^{e}	0.689 (0.120)^{ab}	32.50 (3.70)^{a}
Eshowe	0.657 (0.118)^{bc}	0.406 (0.068)^{bc}	10.62 (3.12)^{bcd}
Last Post	1.407 (0.062)^{a}	0.584 (0.048)^{ab}	20.90 (4.45)^{abc}
Lydenburg	0.594 (0.041)^{bcd}	0.166 (0.048)^{cd}	7.00 (2.48)^{cd}
Modimolle	0.215 (0.054)^{de}	0.054 (0.017)^{d}	4.10 (1.60)^{cd}
Ulundi	1.659 (0.083)^{a}	0.775 (0.047)^{a}	17.40 (5.89)^{abcd}
Wolfaan	0.351 (0.044)^{cde}	0.774 (0.080)^{a}	16.40 (4.06)^{abcd}
ANOVA statistics	F = 47.612, df = 9, $P < 0.001$	F = 15.489, df = 9, $P < 0.001$	F = 6.629, df = 9, $P < 0.001$

Same letters within a column indicate that means are not significantly different.

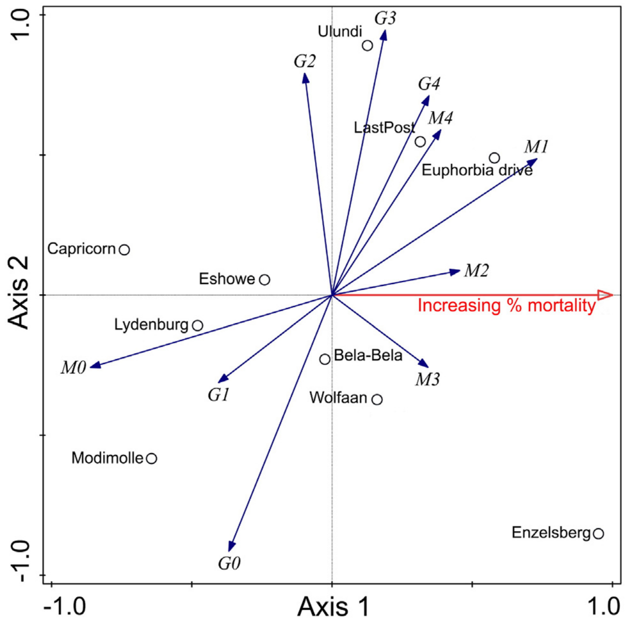

Fig. 4. Redundancy analysis (RDA; pseudo-F = 4.4; P = 0.025) showing relationship among symptoms associated with *Euphorbia ingens* die-off and increasing mortality. G0-G4 indicate scores of graying of *E. ingens* branches with zero being absent to low and 4 being very high. M0-M4 indicate scores of moth damage with zero being absent or low and 4 being very high.

moth damage), as well as mean percentage mortality of *E. ingens* for each transect at each site was calculated and compared using a *t*-test.

To determine whether there had been any significant changes in temperature and precipitation over time at the study sites, ANOVA was used to compare monthly means (minimum and maximum temperatures and precipitation) by decade (1965–1974, 1975–1984, 1985–1994, 1995–2004 and 2005–2014) for all sites except Euphorbia Drive, Eshowe and Ulundi. Temperature data for Euphorbia Drive and precipitation and temperature data for Eshowe and Ulundi were compared for 1996–2005 and 2006–2014 using a Student's *t*-test.

Data were tested for normality using Shapiro–Wilk's W. Kruskal-Wallis one-way ANOVA was used if data were not normal after transformation (ln + 1; to account for zeros in the data). Mean separation tests (Tukey-Kramer's, HSD) were conducted on significant F-tests and H-tests for all interactions. Linear regression analyses, among all sites, were conducted to test if mortality was correlated to any of the soil properties tested in this study. For all tests, α was set at $P \le 0.05$. All statistical analyses were conducted using JMP Version 12.0.1 (SAS Institute Inc., Cary, North Carolina, 1989–2007).

To test for possible spatial auto-correlation between tree die-off symptoms and distance between sites (if closer sites were more alike in symptom severity), we used the RELATE function in PRIMER 6 (PRIMER-E, Lutton, Plymouth, UK), a Mantel-type test that correlates two similarity matrices with one another. For the RELATE test, we used Spearman's Rho with 9999 permutations. The number of trees within each disease category effectively functioned as the 'abundance' of individual trees expressing a symptom at each site. Using the same disease symptom data, we also executed a redundancy analysis (RDA) with the forward selection command in CANOCO 5 (ter Braak and Šmilauer, 2012) to test whether those sites that had higher incidences of moth damage, graying or both also had higher incidences of dead trees in the landscape. Another RDA was performed in CANOCO 5 to observe the principal environmental components that constitute the study sites, after which we used the forward selection function in the CANOCO program to correlate % tree mortality with these site conditions. For both RDA analyses, we used 9999 permutations to calculate correlation coefficients.

3. Results

3.1. Levels and changes over time of Euphorbia ingens die-off symptoms and mortality

Die-off symptoms and mortality were present at all the sites, but occurred at different levels of severity. There was a significant difference in gray discoloration, moth damage and mortality among all the sites investigated (Table 1). Greater tree mortality was significantly correlated with those landscapes where moth damage and gray discoloration were more severe (pseudo-F = 4.4; P = 0.025; Fig. 4). There was no spatial auto-correlation between the symptoms of *E. ingens* die-off and distance between sites (Spearman Rho = −0.05, P = 0.41).

There were significant changes in mortality and die-off factors across both the 4 and 2 year observation periods (Table 2). Only one site (Lydenburg) had no significant change in die-off factors and mortality. Bela-Bela, Enzelsberg, Eshowe, Last Post, and Ulundi all exhibited a marked increase in mortality over the last two to four years. Capricorn,

Table 2
Mean (SE) die-off factor and percentage mortality increase of *Euphorbia ingens* from 2010 to 2014 (Capricorn, Euphorbia Drive, Enzelsberg, Last Post and Wolfaan) and 2012 to 2014 (Bela-Bela, Eshowe, Lydenburg, Modimolle and Ulundi). Significant comparisons in bold.

Site	Year scored	Gray discoloration	*t*-Test result	Moth damage	*t*-Test result	% mortality	*t*-Test result
Bela-Bela	2012	0.724 (0.046)	$t = 1.923$, df = 14, P = 0.075	0.461 (0.107)	$t = 0.018$, df = 14, P = 0.986	6.50 (1.823)	$t = \mathbf{3.062}$, df = **14**, P = **0.008**
	2014	0.560 (0.072)		0.504 (0.082)		14.90 (2.039)	
Capricorn	2010	0.427 (0.104)	$t = -\mathbf{2.346}$, df = **14**, P = **0.034**	0.431 (0.063)	$t = \mathbf{3.581}$, df = **14**, P = **0.003**	0.630 (0.625)	$t = -1.018$, df = 14, P = 0.326
	2014	0.739 (0.082)		0.170(0.028)		2.50 (1.732)	
Euphorbia Drive	2010	1.877 (0.064)	$t = 1.878$, df = 14, P = 0.081	0.889 (0.051)	$t = -\mathbf{2.261}$, df = **14**, P = **0.039**	22.13 (3.476)	$t = -0.547$, df = 14, P = 0.593
	2014	1.695 (0.073)		0.597 (0.055)		25.50 (5.103)	
Enzelsberg	2010	0.036 (0.014)	$t = 1.919$, df = 14, P = 0.076	0.652 (0.071)	$t = 0.263$, df = 14, P = 0.796	14.00 (4.310)	$t = -\mathbf{3.259}$, df = **14**, P = **0.006**
	2014	0.148 (0.056)		0.689 (0.085)		32.50 (3.694)	
Eshowe	2012	0.537 (0.092)	$t = -0.800$, df = 14, P = 0.437	0.384 (0.054)	$t = 0.087$, df = 14, P = 0.932	2.25 (1.521)	$t = -\mathbf{2.366}$, df = **14**, P = **0.033**
	2014	0.657 (0.118)		0.406 (0.067)		10.62 (3.196)	
Last Post	2010	1.311 (0.093)	$t = -0.862$, df = 14, P = 0.403	0.616 (0.037)	$t = 1.066$, df = 14, P = 0.305	2.00 (1.614)	$t = -\mathbf{3.984}$, df = **14**, P = **0.001**
	2014	1.407 (0.062)		0.584 (0.054)		20.90 (4.453)	
Lydenburg	2012	0.529 (0.128)	$t = -0.341$, df = 14, P = 0.739	0.374 (0.133)	$t = 1.470$, df = 14, P = 0.164	4.10 (1.604)	$t = -0.986$, df = 14, P = 0.341
	2014	0.594 (0.141)		0.166 (0.048)		7.00 (2.479)	
Modimolle	2012	0.086 (0.024)	$t = -\mathbf{2.189}$, df = **14**, P = **0.046**	0.040 (0.015)	$t = -0.434$, df = 14, P = 0.671	3.40 (1.603)	$t = -0.331$, df = 14, P = 0.745
	2014	0.215 (0.054)		0.054 (0.016)		4.10 (1.597)	
Ulundi	2012	1.284 (0.079)	$t = -\mathbf{3.279}$, df = **14**, P = **0.005**	0.556 (0.036)	$t = -\mathbf{3.366}$, df = **14**, P = **0.005**	3.40 (2.442)	$t = -\mathbf{2.196}$, df = **14**, P = **0.045**
	2014	1.659 (0.083)		0.775 (0.050)		17.40 (5.889)	
Wolfaan	2010	0.205 (0.096)	$t = -1.381$, df = 14, P = 0.189	0.122 (0.067)	$t = -\mathbf{5.756}$, df = **14**, P < **0.001**	6.30 (2.833)	$t = -2.045$, df = 14, P = 0.060
	2014	0.351 (0.044)		0.774 (0.075)		16.40 (4.062)	

Modimolle and Ulundi showed a significant increase in gray discoloration while Ulundi and Wolfaan showed a significant increase in moth damage. Capricorn and Euphorbia Drive showed a significant decrease in moth damage over the last four years.

3.2. Precipitation and temperature

Significant site-specific changes were observed for minimum temperature, maximum temperature and precipitation (Table 3). Lydenburg

Table 3
Results of analyses (ANOVA, Kruskal-Wallis one-way ANOVA and *t*-test) of monthly mean minimum temperature, maximum temperature and precipitation (per decade) from 1965 to 2014 (Bela-Bela, Capricorn, Euphorbia Drive, Enzelsberg, Last Post, Lydenburg, Modimolle and Wolfaan) and from 1996 to 2014 (Euphorbia Drive, Eshowe and Ulundi).

Site	Decade	Mean minTemp (°C) (SD)	Result	Mean maxTemp (°C) (SD)	Result	Precipitation (mm) (SD)	Result
Bela-Bela	1965–1974	11.22^{a}	H = **11.871**, df = **4**, P = **0.018**	26.52^{b}	H = **21.415**, df = **4**, P < **0.001**	603.77	H = 2.839, df = 4, P = 0.585
	1975–1984	10.72^{b}		26.55^{b}		692.39	
	1985–1994	11.50^{a}		27.06^{b}		612.33	
	1995–2004	11.34^{a}		27.09^{b}		631.31	
	2005–2014	11.59^{a}		28.8^{a}		572.93	
SE		**0.162**		**0.238**		**48.98**	
Capricorn	1965–1974	12.45	H = 5.102, df = 4, P = 0.277	26.8^{c}	H = **22.159**, df = **4**, P < **0.001**	429.71	H = 3.824, df = 4, P = 0.430
	1975–1984	12.00		27.03^{bc}		513.43	
	1985–1994	12.34		27.70^{ab}		416.81	
	1995–2004	12.50		27.48^{bc}		510.86	
	2005–2014	12.35		28.25^{a}		414.83	
SE		**0.174**		**0.182**		**47.98**	
Euphorbia Drive	1996–2005	13.74 (0.499)	*t* = **2.641**, df = **17**, P = **0.017**	27.60 (0.872)	*t* = −1.950, df = 17, P = 0.068		H = 4.539, df = 4, P = 0.338
	2006–2014	13.12 (0.527)		28.22 (0.425)			
	1965–1974					553.37	
	1975–1984					567.89	
	1985–1994					478.78	
	1995–2004					545.35	
	2005–2014					530.44	
SE						**35.70**	
Enzelsberg	1965–1974	11.72	F = 2.727, df = 4, P = 0.076	27.27^{b}	F = **7.624**, df = **4**, P < **0.001**	602.14	H = 3.135, df = 4, P = 0.535
	1975–1984	12.21		27.31^{b}		591.3	
	1985–1994	11.50		29.86^{a}		569.52	
	1995–2004	11.97		26.98^{b}		665.04	
	2005–2014	11.83		28.35^{a}		517.08	
SE		**0.177**		**0.429**		**56.948**	
Eshowe	1996–2005	16.66 (0.503)	*t* = 1.999, df = 17, P = 0.062	27.43 (0.521)	*t* = −0.168, df = 17, P = 0.868	1203.44 (258.19)	*t* = −0.010, df = 17, P = 0.993
	2006–2014	15.94 (1.011)		27.48 (0.654)		1204.87 (388.20)	
Last post	1965–1974	12.45	H = 5.102, df = 4, P = 0.277	26.8^{c}	H = **22.159**, df = **4**, P < **0.001**	429.71	H = 3.824, df = 4, P = 0.430
	1975–1984	12.00		27.03^{bc}		513.43	
	1985–1994	12.34		27.70^{ab}		416.81	
	1995–2004	12.50		27.48^{bc}		510.86	
	2005–2014	12.35		28.25^{a}		414.83	
SE		**0.174**		**0.182**		**47.98**	
Lydenburg	1965–1974	9.28^{b}	F = **29.888**, df = **4**, P < **0.001**	22.73^{c}	H = **20.405**, df = **4**, P < **0.001**	680.57^{a}	H = **25.381**, df = **4**, P < **0.001**
	1975–1984	9.26^{b}		23.10^{bc}		740.04^{a}	
	1985–1994	10.24^{a}		23.06^{bc}		745.28^{a}	
	1995–2004	10.38^{a}		23.34^{ab}		350.26^{b}	
	2005–2014	10.36^{a}		23.81^{a}		424.00^{b}	
SE		**0.109**		**0.145**		**48.89**	
Capricorn	1965–1974	12.45	H = 5.102, df = 4, P = 0.277	26.8^{c}	H = **22.159**, df = **4**, P < **0.001**	429.71	H = 3.824, df = 4, P = 0.430
	1975–1984	12.00		27.03^{bc}		513.43	
	1985–1994	12.34		27.70^{ab}		416.81	
	1995–2004	12.50		27.48^{bc}		510.86	
	2005–2014	12.35		28.25^{a}		414.83	
SE		**0.174**		**0.182**		**47.98**	
Ulundi	1996–2005	14.33 (0.340)	*t* = 1.416, df = 17, P = 0.175	26.61 (0.650)	*t* = 1.125, df = 17, P = 0.276	641.77 (136.58)	*t* = 0121, df = 17, P = 0.905
	2006–2014	13.71 (1.345)		26.22 (0.851)		630.82 (248.70)	
Wolfaan	1965–1974	10.94^{b}	F = **12.719**, df = **4**, P < **0.001**	26.42^{ab}	H = **13.572**, df = **4**, P = **0.009**	704.17	F = 0.767, df = 4, P = 0.553
	1975–1984	11.25^{b}		25.88^{b}		678.55	
	1985–1994	11.21^{b}		26.29^{ab}		549.95	
	1995–2004	11.82^{b}		26.30^{ab}		611.17	
	2005–2014	13.94^{a}		26.96^{a}		574.62	
SE		**0.343**		**0.196**		**75.52**	

SD = standard deviation.
SE = standard error.
Same letters within a column, specific to a site, indicate that means are not significantly different.

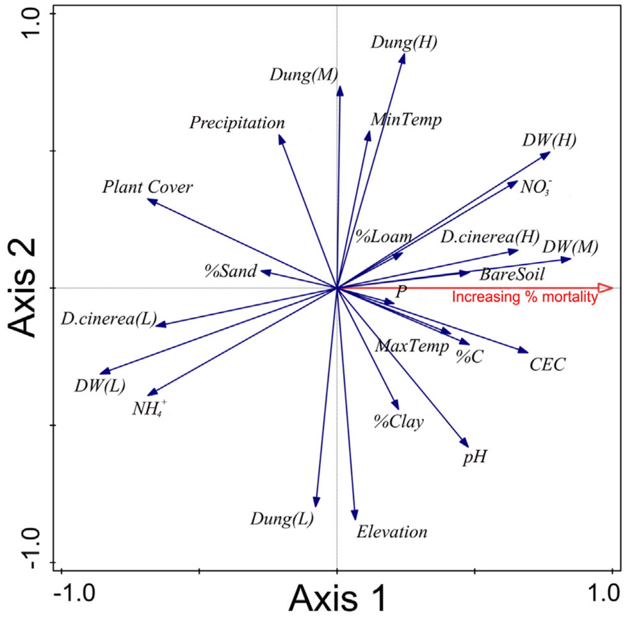

Fig. 5. Redundancy analysis (RDA; pseudo-F = 2.7; P = 0.003) showing increasing mortality of *Euphorbia ingens* in relation to landscape variables scored in this study. DW = dead woody debris, *D. cinerea* = *Dichrostachys cinerea*, CEC = soil cation-exchange capacity, %C = % soil carbon, precipitation = monthly mean precipitation, minTemp = monthly mean minimum temperature and maxTemp = monthly mean maximum temperature. H, M and L in parentheses are High, Medium or Low. Bare soil, higher levels of dead wood and high levels of *D. cinerea* encroachment were associated with increased mortality (more diseased sites) while higher grass cover, lower levels of dead wood and lower levels of *D. cinerea* encroachment were associated with healthier sites (low levels of *E. ingens* mortality).

changed the most with a significant increase in minimum and maximum temperatures and a significant decrease in precipitation. There was a significant increase in minimum temperature at Bela-Bela, Lydenburg, Modimolle and Wolfaan, while at Euphorbia Drive, minimum temperature decreased significantly. Maximum temperature increased significantly across all sites except Euphorbia Drive, Eshowe and Ulundi. Except for Lydenburg, there was no significant change in precipitation. Increased percentage tree mortality was generally associated with sites that had overall higher temperatures and less rainfall.

3.3. *Euphorbia ingens* mortality and landscape degradation

Higher levels of *E. ingens* mortality were associated with landscape parameters that are indicative of land degradation. Sites with the highest levels of *E. ingens* mortality displayed clear characteristics of degradation (high levels of bare soil, high levels of dead wood, higher dung counts and high bush encroachment by *D. cinerea*) (pseudo-F = 2.7; P = 0.003; Fig. 5). These severely diseased sites (Enzelsberg, Euphorbia Drive, Last Post and Ulundi) were overgrazed with low levels of living grass cover and *E. ingens* trees were severely encroached with *D. cinerea*. Sites with the lowest levels of mortality (Capricorn, Eshowe, Lydenburg and Modimolle) were associated with high levels of living plant cover (specifically grass cover) with low levels of dead wood and low levels of *D. cinerea* encroachment (Fig. 6). Sites with higher levels of *E. ingens* die-offs were correlated with high levels of nitrates ($P = 0.043$, $R^2 = 0.419$) and CEC ($P = 0.024$, $R^2 = 0.492$). The other soil characteristics tested were not significantly correlated to *E. ingens* mortality; ammonium ($P = 0.660$, $R^2 = 0.025$), carbon ($P = 0.201$, $R^2 = 0.194$), clay ($P = 0.553$, $R^2 = 0.046$), loam ($P = 0.508$, $R^2 = 0.057$), pH ($P = 0.148$, $R^2 = 0.242$), phosphorus ($P = 0.681$, $R^2 = 0.022$) and sand ($P = 0.446$, $R^2 = 0.074$) (Table 4).

4. Discussion

Previous studies have described the insects and pathogens that are associated with mortality of *E. ingens* in areas experiencing die-off. But none of these agents were considered primary pathogens or pests (Van der Linde et al., 2011a, 2011b, 2011c). This suggests that some factor is predisposing *E. ingens* to attacks by these otherwise secondary insects and pathogens. Although evidence exists linking climate change to the die-off (Van der Linde et al., 2012), we show here that disease symptoms and mortality could also be explained by savanna degradation. While there were significant changes in temperature and precipitation at most of the sites in this study, these changes did not necessarily relate to symptom and die-off severity. This challenges the role of climate as the only trigger that has led to *E. ingens* die-offs. For example, Ulundi, which exhibited a significant increase in symptoms and mortality, experienced no significant change in temperature and precipitation over the last 20 years. Likewise, Lydenburg, which had a significant increase in minimum temperature, maximum temperature and a decrease in precipitation, showed no significant increase in symptoms or mortality. Capricorn, which had a significant increase in maximum temperature, was one of the healthiest sites included in this study with a mean percent morality of only 2.5%.

Landscape parameters that indicate savanna disturbance were highly correlated with *E. ingens* mortality across sites. Since livestock farming (subsistence and commercial) is an established activity in these landscapes, the observed rates of mortality suggest that *E. ingens* trees are negatively affected by this activity. The stress from intensive livestock grazing could predispose *E. ingens* populations to insect and pathogen damage and could eventually lead to local extinction.

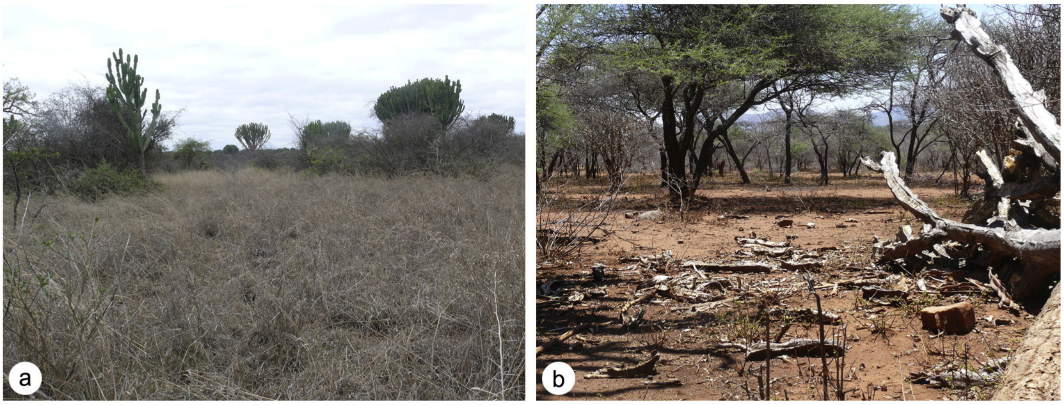

Fig. 6. Comparison of a typical site where *Euphorbia ingens* mortality is low and high. (a) Capricorn (*E. ingens* mortality 2.5%); high level of live ground plant cover and hardly any *Dichrostachys cinerea* encroachment. (b) Euphorbia Drive (*E. ingens* mortality 25.50%); high levels of bare soil and *D. cinerea* encroachment.

Table 4
Soil characteristics tested and results from each site investigated in the current study.

Site	pH	P (mg/kg)	NO_3^- mg/kg	NH_4^+ mg/kg	CEC cmol(+)/kg	% carbon	% sand	% loam	% clay
Bela-Bela	6.19	11.91	8.72	6.97	19.1	2.28	69	11	20
Capricorn	6.4	4.05	4.94	6.9	22.1	0.63	81	7	12
Euphorbia drive	7.47	4.05	9.59	5.22	23.06	1.4	62	19	19
Enzelsberg	6.82	7.88	11.17	6.55	24.44	1.61	68	17	15
Eshowe	5.89	11.91	7.42	5.08	16.64	1.47	67	18	15
Last post	6.4	17.78	8.58	14.28	25.31	1.59	75	15	10
Lydenburg	6.57	7.25	8.93	5.64	17.28	1.4	55	29	16
Modimolle	6.23	4.49	8.61	7.42	14.55	0.68	81	6	13
Ulundi	5.85	12.16	12.57	11.03	19.79	1.19	78	10	12
Wolfaan	6.31	39.97	9.8	6.09	20.58	2.56	70	14	16

P = phosphorus, NO_3^- = nitrate, NH_4^+ = ammonium, CEC = cation exchange capacity.

While climate change may play a role in the die-off, our results indicate that ecosystem degradation very likely exacerbates and may even trigger *E. ingens* die-offs.

Euphorbia ingens has a shallow root system typical of succulent-type plants in a xeric environment (Van Wyk and Van Wyk, 1997; Palgrave et al., 2002). This type of root system allows the plants to rapidly access moisture in rare wet events. High livestock stocking rates would lead to compaction of the soil that could damage roots, restricting moisture and nutrient uptake and it could place *E. ingens* under further stress (Rietkerk et al., 1997, 2000; Van Langevelde et al., 2003). Apart from physical damage to the roots by the grazers, crust formation occurs (causing soil erosion and run-off) leading to the possibility of less water availability at the root level (Kelly and Walker, 1976; Rietkerk et al., 1997, 2000; Van Langevelde et al., 2003; Savadogo et al., 2007). Results of this study showed that sites with high levels of *E. ingens* mortality had the highest concentrations of NO_3^- and CEC in the soil, contradicting the fact that the soil might have lowered water retention and nutrient availability at these specific sites. CEC measures the soil's ability to hold exchangeable cations and the availability of important nutrients to plants, with higher CEC values linked to fertile soils with good water retention (Bot and Benites, 2005; Saidi, 2012). Water in the soil is needed to convert organic nitrogen to ammonium (NH_4^+) which is eventually converted to nitrates (NO_3^-), which provide plants with their most usable form of nitrogen (Anthonisen et al., 1976). Therefore, low levels of NO_3^- usually indicate low levels of water in the soil (Anthonisen et al., 1976). Nutrient uptake ability, due to damaged roots and compaction, might be the more likely stress factor. Furthermore, water and nutrient availability to *E. ingens* trees can also be reduced due to uptake and competition by *D. cinerea* in areas where it has encroached on *E. ingens* habitat (Rietkerk et al., 1997, 2000; Van Langevelde et al., 2003; Savadogo et al., 2007).

The knowledge that habitat degradation is likely involved in *E. ingens* die-offs is important because it indicates that appropriate rangeland management of xeric savannas could aid in conserving *E. ingens* in the landscape. This is especially relevant because other indicated causes of *E. ingens* die-off, such as climatic variability, are far less practical to mitigate. An attempt to sustainably manage the studied savanna landscapes may not only help to conserve this iconic tree species, but it will also aid biodiversity conservation ideals in general, since many more species are inevitably affected by such landscape degradation.

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