Contemporary and historical impacts of megaherbivores on the population structure of tree euphorbias in South African subtropical thicket

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Abstract

African elephant and black rhinoceros – both megaherbivores – impact negatively on the abundance of succulent plants, including tree succulents, in South Africa's subtropical thicket. We sampled 35 sites in subtropical thicket to assess historical and contemporary impacts of African elephant and black rhinoceros on the population structure of three species of succulent tree euphorbia. Population age structures were highly variable and showed no species-specific effects. Almost half the sites had growing populations dominated by young individuals. Sites having contemporary impacts had significantly fewer individuals in the 30–75 years age range, but this effect declined with increasing terrain slope. Eighty-one percent of sites assumed to have been impacted by megaherbivores historically had individuals that predated rhino and elephant extirpation in the region. This and other population age structure data indicate that megaherbivores and tree euphorbias coexisted historically on terrain of low relief. However, in areas not subject to contemporary impacts, euphorbia populations are likely to be much higher now than historically, owing to population relaxation after the extirpation of megaherbivores in the mid 1800s. Given the sensitivity of tree euphorbias to megaherbivore impacts, managers should consider monitoring the population structure of these species in order to identify thresholds of potential concern regarding megaherbivore impacts.

Key words: African elephant, black rhinoceros, population relaxation, size preference, topographic effects

Résumé

L'éléphant et le rhinocéros africains – deux méga-herbivores – ont un impact négatif sur l'abondance de plantes succulentes, y compris des arbres succulents, dans les fourrés subtropicaux d'Afrique du Sud. Nous avons prélevé des échantillons dans 35 fourrés subtropicaux afin d'évaluer les impacts anciens et actuels des éléphants et des rhinos noirs africains sur la structure de la population de trois espèces d'euphorbes arborescentes succulentes. Les structures d'âges des populations étaient très variables et ne présentaient aucun effet spécifique des espèces. Près de la moitié des sites contenaient des populations en croissance dominées par de jeunes individus. Les sites qui présentaient des impacts actuels comptaient significativement moins d'individus de la classe d'âge comprise entre 30 et 75 ans, mais cet effet diminuait lorsque la pente du terrain s'accentuait. Quatre-vingt-un pour cent des sites supposés avoir subi jadis l'impact des méga-herbivores contenaient des individus qui dataient d'avant l'élimination des rhinos et des éléphants. Ceci, tout comme d'autres données sur la structure d'âge des populations, indique que les méga-herbivores et les euphorbes arborescentes ont longtemps coexisté sur les terrains de faible relief. Cependant, dans les zones qui ne subissent aucun impact actuel, les populations d'euphorbes sont susceptibles d'être beaucoup plus hautes aujourd'hui que jadis, en raison de la libération induite par l'élimination des méga-herbivores au milieu des années 1800. Etant donné la sensibilité des euphorbes arborescentes face aux impacts des méga-herbivores, les gestionnaires devraient envisager le suivi continu de la structure de la population de ces espèces afin de déterminer les seuils d'alerte potentiels en ce qui concerne les impacts des méga-herbivores.

Introduction

At high densities, African elephant (*Loxodonta africana* Blum.) – a megaherbivore (Owen-Smith, 1998) – can

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greatly alter the appearance of vegetation, notably by reducing the density of large trees (e.g. Laws, 1970; Western & Maitumo, 2004) but also by impacting on other ecosystem components (Moolman & Cowling, 1994; Cumming *et al.*, 1997; Kerley & Landman, 2006). The impacts on ecosystems of black rhinoceros (*Diceros bicornis minor* L.) – another megaherbivore – has been less studied; available evidence indicates that where succulent members of the genus *Euphorbia* coexist with these rhinos, they target them, impacting on populations of tree-like species (tree euphorbias) by pushing them over to consume the growing tips (Goddard, 1968; Dudley, 1997; Heilmann *et al.*, 2006). There is a great deal of controversy as to whether elephant impacts on vegetation structure, species diversity and ecosystem processes should be regarded as undesirable, or whether they are reversible states whose trajectories are governed by fluctuations in megaherbivore population sizes (Owen-Smith *et al.*, 2006). Central to this controversy is the identification of appropriate benchmark states: what did the vegetation look like prior to the local extirpation of megaherbivores in many parts of Africa during the early phases of the colonial period (Cowling & Kerley, 2002; Owen-Smith *et al.*, 2006).

The Subtropical Thicket Biome of South Africa's Eastern Cape Province poses a particular challenge regarding megaherbivore impacts. At high densities locally, megaherbivores impact negatively on the abundance of the biomes' succulents and geophytes (Moolman & Cowling, 1994; Lombard *et al.*, 2001; Heilmann *et al.*, 2006), many of which are species of special conservation concern (Johnson, Cowling & Phillipson, 1999). Megaherbivores are currently being reintroduced at a rapid pace into the numerous but relatively small statutory and privately owned protected areas scattered throughout this biome (Kerley & Landman, 2006). Identifying benchmark states as a component of monitoring programmes for evaluating megaherbivore impacts is therefore a key research topic.

Both elephant and black rhinoceros were common in subtropical thicket in precolonial times (Skead, 2007). While difficult to corroborate, it is estimated that this region may have once supported tens of thousand of elephants (Boshoff, Skead & Kerley, 2002); precolonial rhino numbers are unknown. During the eighteenth and early nineteenth century, herds of elephant in excess of several hundred individuals were commonly observed on the coastal forelands and river valleys of the immediate hinterland, or sub-coastal sector (Boshoff, Skead & Kerley, 2002). Ivory hunters entered the region in the 1730s and

by the late 1700s, the elephant population was already declining. By the 1840s, save for a population at Addo, elephants were extinct in the region; the last rhino was shot in 1858 (Skead, 2007).

Tree euphorbias (and tree aloes) are a conspicuous feature of contemporary subtropical thicket landscapes, especially on the flanks and floors of the incised valleys of the coastal plain (Vlok, Euston-Brown & Cowling, 2003). Unlike woody shrubs and trees of thicket, which are very long-lived and are predominantly ramet recruiters – tree euphorbias are relatively short-lived (200–300 years), do not sprout after disturbance (Heilmann *et al.*, 2006), and produce numerous seedlings (Midgley & Cowling, 1993). Given the facility with which individuals can be aged (owing to the presence of stem annuli), and that their lifespans extend beyond colonial extirpation of megaherbivores, tree euphorbias provide a good opportunity to assess historical (and contemporary) impacts of megaherbivory (O'Connor, Goodman & Clegg, 2007). Here we investigated the population age structure of three tree euphorbias – *Euphorbia grandidens* Haw., *E. tetragona* Haw. and *E. trangularis* Desf. – in 35 sites in the subtropical thicket of the Eastern Cape, South Africa. Firstly, we described and classified the population characteristics of the sample sites. Next we compared the age structure of populations in relation to megaherbivores impact regimes, namely contemporary impact, historical (pre-extirpation) impact, and no impact (i.e. sites associated with very steep slopes). We also assessed the role of increasing site slope (as a surrogate for megaherbivore impacts) on age structure of sites currently impacted compared to sites impacted historically. Finally, we scrutinized the population age structure curves for bimodalities that would indicate historical megaherbivore impacts and subsequent postextirpation population relaxation.

Materials and methods

Study area

We delineated our study area (Fig. 1) as follows. First we identified the area encompassing subtropical thicket vegetation types mapped by Vlok, Euston-Brown and Cowling (2003) that had a high probability of supporting populations of any one of the three tree euphorbias. These were variants of Valley Thicket (400–500 mm year^{-1}) (*E. grandidens, E. tetragona*) and Thicket (500–700 mm year^{-1}) (*E. triangularis*). Then we constrained the area to encompass the
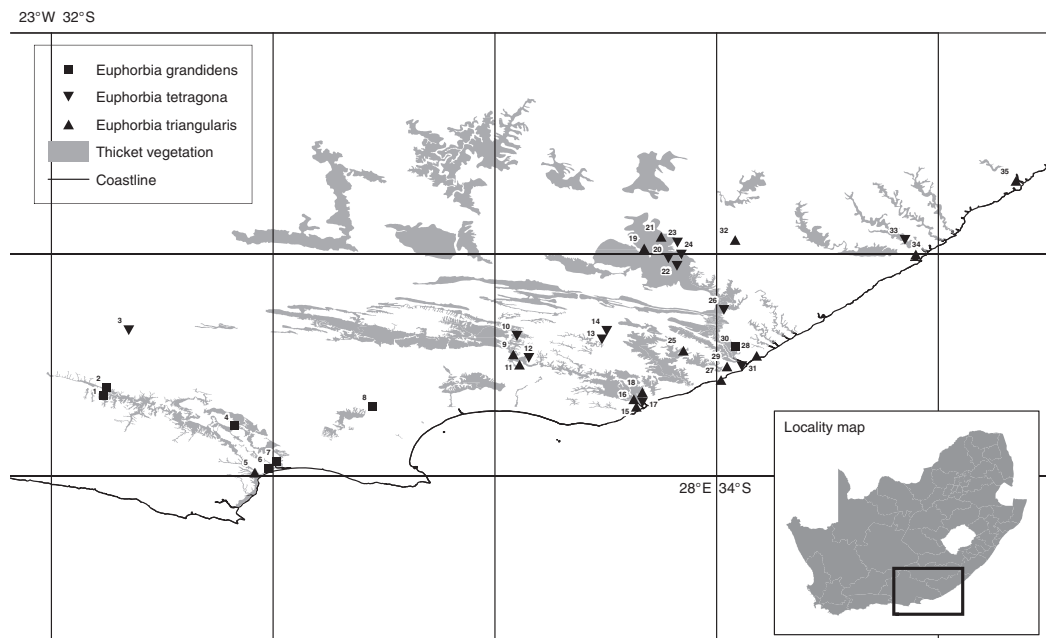
Fig 1 Map of the study area showing the location of sites sampled for assessing the population age structure of three tree *Euphorbia* species in Eastern Cape subtropical thicket. Mapped thicket comprises Valley Thicket and Thicket types according to Vlok, Euston-Brown and Cowling (2003) that support populations of the three *Euphorbia* species. Sampled areas include those that are likely to have supported large populations of megaherbivores (elephant and black rhinoceros), at least intermittently (Boshoff, Skead and Kerley, 2002)

coastal and sub-coastal belts delineated by Boshoff, Skead and Kerley (2002): in the former region, elephants were resident and widespread in precolonial times, whereas in the latter region, they were restricted to river valleys clad in subtropical thicket, the habitat of interest to us (Skead, 2007). Historical records suggest that black rhinoceros was a common resident in the subtropical thicket of both the coastal and sub-coastal belts (Skead, 2007).

Data collection

We identified three megaherbivore impact regimes, namely no impact (NI), historical impact (HI) and contemporary impact (CI). We regarded as NI sites those on very steep slopes (>30°) where large-bodied megaherbivores would have negligible impact (Heilmann *et al.,* 2006; Edkins *et al.,* 2007). HI sites were those on level to moderate (0–30°) terrain that we assumed had supported – at least intermittently – populations of the two megaherbivores in precolonial times. CI sites were those on level to moderate terrain where megaherbivores had been reintroduced in the last 20 years. In order to assess whether slope had any effect on megaherbivore impacts, we categorized the HI

and CI sites as level (0–5°), gentle (5–10°) and moderate slope (10–20°).

We sampled 35 sites across the study area in 2002/3, four being NI, nineteen HI and twelve CI. Of the last-mentioned, black rhinoceros have been re-introduced to eight sites and elephant to four; both species have been re-introduced to only one site. We avoided sites that had been heavily impacted by livestock grazing. We acknowledge that our sampling strategy poses challenges for discerning patterns in population structure in relation to impact regime. Historical megaherbivore populations and associated impacts are likely to have fluctuated locally (Boshoff, Skead and Kerley, 2002) and CI sites vary according to residence time, population size and species of introduced megaherbivore. Furthermore, a host of constraints meant that it was not possible to have equal sample sizes for combinations of impact regime, slope and species. Thus, for *Euphorbia grandidens*: NI = 0 sites, HI = 7 (1 level, 2 gentle, 4 moderate) and CI = 0; *E tetragona*: NI = 2 sites, HI = 3 (all moderate) and CI = 8 (6 level, 1 gentle, 1 moderate); *E. triangularis*: NI = 2 sites, HI = 9 (2 level, 7 gentle) and CI = 4 (1 level, 2 gentle, 1 moderate). However, since the three tree euphorbias showed similar

population structures (Table 1), we subsequently treated these data as coming from a single population. This reduced imbalance in the sampling design.

At each site, we selected a dense population of tree euphorbia and sampled all individuals in a 10×20 m plot. Sampled densities across all sites and species ranged from 30 to 101; mean (SD) and median densities were 84.9 (18.8) and 94, respectively. For each individual, we estimated age as the number of growth rings on the annulated stem, assuming that each annulus represented one year's growth. Our observations of plants in cultivation over a five-year period provided support for this assumption. However, annuli become indistinct in the lowest third of the stem in older individuals (>100 years) and are generally easier to detect for *Euphorbia tetragona* than the other two species. Hence, there is likely to be considerable error in assigning exact ages to older individuals. Consequently, we allocated individuals >120 years to 10-years bins, and >200 years to 20-years bins.

Data analysis

We depicted the population-age data for each site as kernel density plots. Kernel density estimation (Silverman, 1986; Hastie, Tibshirani & Friedman, 2001) has largely supplanted the histogram as a method for estimating the distribution of univariate data. The method uses a weighting scheme (the kernel) and a bandwidth (a metrical 'window' in which the weighting scheme works) to make a locally determined estimate of occurrences by weighting data points according to how far they are from the value being estimated. The traces in the kernel density plots, therefore, show an estimate of where in the line of observed values of age the observations accumulate. We used a Gaussian kernel with Silverman's (1986) 'rule-of-thumb' bandwidth for density estimation.

In order to assess the effects of impact regime and slope on age structure, we combined data from all sites and for all euphorbia species within each of the impact regime/slope categories. We inspected the raw data to ensure that by combining populations thus, we had not created artificial bimodality, for example, by combining a site having a left-skewed age distribution with a site having a right-skewed age distribution (e.g. sites 10 and 20 in Fig. 2b). To do this in an unbiased way we used cluster analysis to identify and exclude atypical sites. We thus excluded seven sites, two from CI/level (sites 10 and 20), two from HI/gentle (sites 7 and 25), and three from HI/moderate (sites 4, 26 and 30) (see Fig. 2).

We tested the null hypothesis that megaherbivore impact regime would have no effect on tree euphorbia population age structure. We did this by fitting hierarchical log-linear models (Haberman, 1972) to contingency tables of counts of age classified by impact regime and slope. The model fitting is equivalent to using a Poisson regression with a log link to model the count data for age using megaherbivore impact regime and slope as the explanatory variables (Agresti, 2002). We summarized the results using association plots (Friendly, 1994). These show the Pearson residuals from a fitted model as rectangles. Each rectangle represents a cell in the underlying contingency table and is sized so that its area is proportional to the difference between the observed and expected value of the cell it represents, according to a particular model of independence. A baseline shows the point of independence; rectangles that project above it indicate a greater number of observed values than expected, those that project below it indicate a fewer number of observed values than expected.

We conducted two main analyses. In the first, we assessed the effect of impact regime (CI, HI and NI) over the full age spectrum, ignoring slope. However, it must be borne in mind that the NI sites were – per definition – exclusively associated with steep slopes. In the second analysis, we compared the effect of impact regime on a slope-by-slope basis (i.e. within slope categories) for the CI and HI regimes. For the second analysis, we truncated age

Table 1 Salient characteristics of the entire populations of three tree euphorbias sampled in subtropical thicket

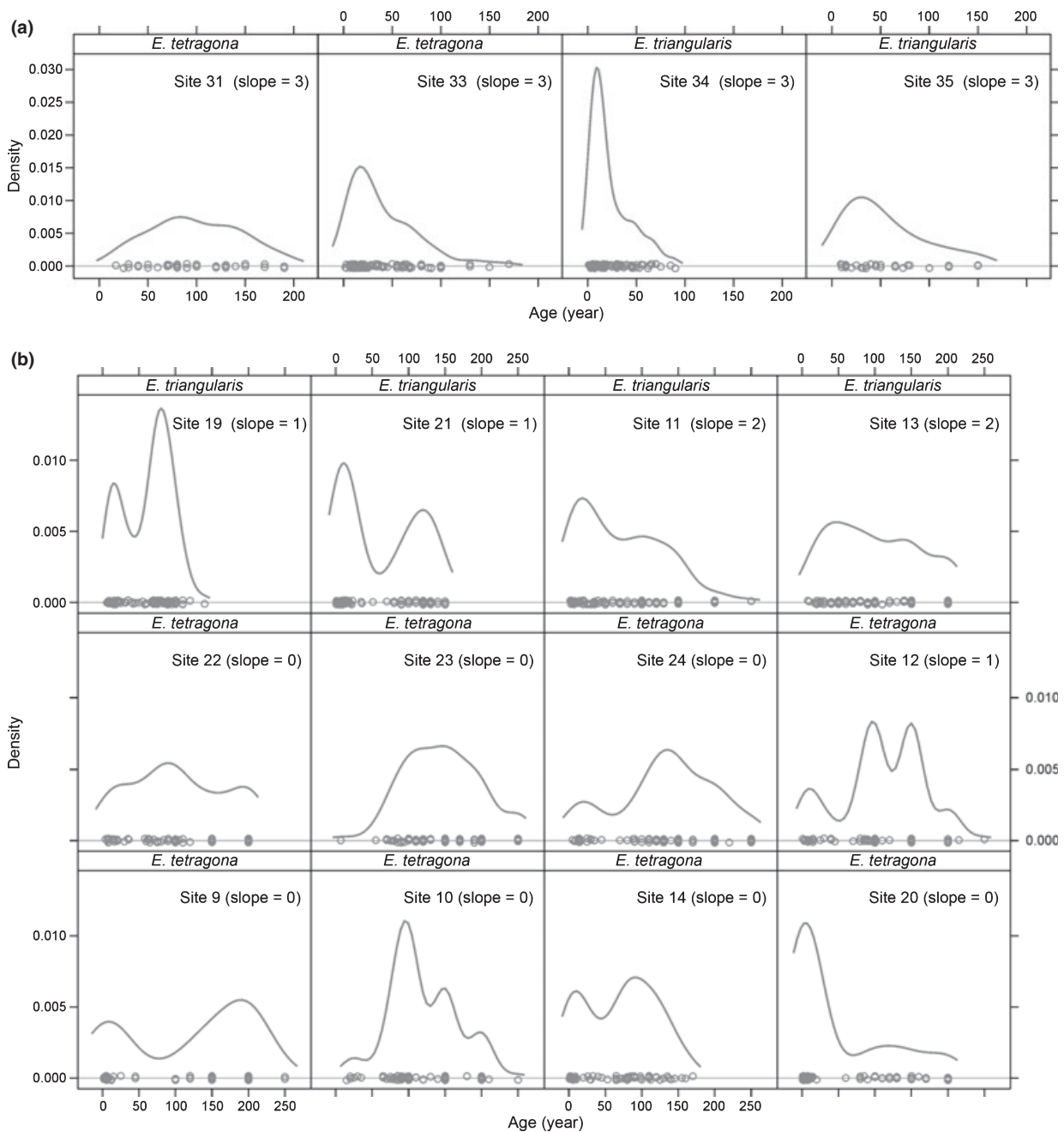|	Age (years)				Age (years) (%)			
	Total	Median	Mean	SD	1–47	48–105	106–180	181–280
E. grandidens	563	80	80.3	61.3	36	33	23	8
E. tetragona	1070	100	99.7	70.3	29	27	26	17
E. triangularis	1337	70	81.4	67.0	38	31	17	13

Fig 2 Kernel density plots showing age frequency distributions for three tree euphorbia species in Eastern Cape subtropical thicket. Sites are grouped according to megaherbivore impact regime: (a) no impact (NI – steep slopes), (b) contemporary (CI) and (c) historical impact only (HI). Slope 0 = level, slope 1 = gentle, slope 2 = moderate, slope 3 = steep. Site numbers are those depicted in Fig. 1. A jittered rugplot at the base of each plot shows the actual data points

to 100 years or less because the first analysis showed considerable fewer individuals than expected in the CI regime in many classes spanning the age range ca.

30–75 years. Therefore, we focused more closely on this part of the age range and tested the hypothesis that increasing slope would reduce the contrast between the

(c)

Fig 2 Continued

two impact regimes, since megaherbivores avoid steeper slopes (Heilmann *et al.,* 2006; Edkins *et al.,* 2007). To do this, we used a Cochran–Mantel–Haenszel (CHM) test to assess whether the HI and CI impact regimes have the same effect across slope categories, and Pearson's Chi-square to determine the contribution of different slope categories to the overall effect. *P* values were empirically derived using Monte-Carlo methods (100 000 re-samplings).

We assessed historical impacts by inspecting the population age structure data at the site scale. First, we counted the number of individuals of tree euphorbia older than 175 years on level, gentle and moderate slopes. Since hunting intensified in the late 1700s and extirpation of

both elephant and black rhinoceros had occurred by the mid 1800s (Skead, 2007), these data would provide an indication of the extent to which tree euphorbias coexisted with relatively large (precolonial) population densities of megaherbivores (cf. Boshoff, Skead and Kerley, 2002). Second, we scrutinized the CI and HI sites for a signal of historical megaherbivore impacts. Given that megaherbivores select younger (and smaller) tree euphorbia individuals (Heilmann *et al.* 2006; this study), thereby increasing the mortality rate in this cohort, we would expect to see a trough in the population-age structure for sites that were historically exposed to megaherbivore impacts. The age of this trough would indicate – albeit crudely – the date of megaherbivore extirpation.

Statistical analysis was carried out using R (R Development Core Team, 2008), supplemented by the contributed package coin (Hothorn *et al.*, 2006) and vcd (Meyer, Zeileis & Hornik, 2006).

Results

Population characteristics

We sampled 2970 individuals of tree euphorbia, the highest numbers for *Euphorbia triangularis* (1337), followed by *E. tetragona* (1070) and *E. grandidens* (563). The youngest plants recorded were ≤1 year-old (all species) whereas the oldest was approximately 280 years (*E. tetragona*). Overall, the three species had similar population characteristics: median ages ranged from 70 to 100 years; and age structures showed a broadly similar pattern, with the highest proportion of individuals less than 50 years and the lowest in the oldest age class (Table 1). *E. grandidens* had the lowest proportion (1.1%) of seedlings (≤5 years); corresponding data were 8.4% for *E. triangularis* and 12.1% for *E. tetragona*.

At the site level, there was a great deal of variation in population age structure and no consistent species-specific patterns were evident (Fig. 2). Sixteen (46%) sites could be characterized as growing populations with a predominance of young individuals (<10 years old); the remainder had relatively few young individuals. Eight (23%) sites had unimodal age structures, twelve (34%) had reverse J-shaped curves, and fifteen (43%) had bi- or tri-modal distributions.

Megaherbivore impacts

Relative to the HI and NI regimes, there were significantly fewer individuals in most year classes between 30 and 75 years than expected in the CI regime, and significantly more than expected in some classes between 100 and 150 years (Fig. 3). Both the HI and NI regimes had more individuals in the 30–75 years bracket than expected. Generally, the NI regime had more young individuals and fewer of the oldest than expected.

Overall, the frequency of individuals in the 30–75 years age class was significantly influenced by megaherbivore impact regime (CI versus HI) as conditioned by slope (Generalized Cochran–Mantel–Haenszel $\chi^2 = 81.19$, $P = 2e-16$). Separate analyses (Pearson's χ^2 tests) for each slope showed, however, that the two impact regimes were significantly different only for the level and gentle categories. As indicated by the association plot (Fig. 4), differences for the moderate slope category were not significant ($\chi^2 = 13.88$ and $P = 0.205$). Thus, on moderate slopes, the CI impact regime loses its characteristic 'dip' in the 30–75 year range (Fig. 3) and comes to resemble the HI impact regime (Fig. 2b,c).

Twenty-five (81%) of the sites that we assumed to have been exposed to megaherbivore impacts historically (CI and HI) supported tree euphorbias older than 175 years. These comprised 405 (15% of total) tree euphorbia individuals. The mean age of these individuals was 206, indicating that most would have established in the beginning of the nineteenth century, when hunting intensity was beginning to escalate, but megaherbivore population sizes were likely to have been substantial.

A total of fifteen sites (43%) had bi- or tri-modal population age structure (all associated with CI and HI regimes). Six of these had bimodal age distributions, showing the dearth of individuals in the 30–75 years range, characteristic of the CI regime. However, nine had distributions with low numbers of individuals associated with the 150–200 years age range (sites 2, 10, 12, 16, 18, 24, 28, 29, 32 in Fig. 2b,c), suggesting that extirpation occurred between 1800 and 1850.

Discussion

Population characteristics

Overall, each of the three tree euphorbia species showed a wide range of population age structures: there was no evidence of species-specific patterns. Almost half the sites had reverse J-shaped distributions with peak numbers of seedlings and juveniles, corroborating observations by Midgley & Cowling (1993) that tree euphorbias – along
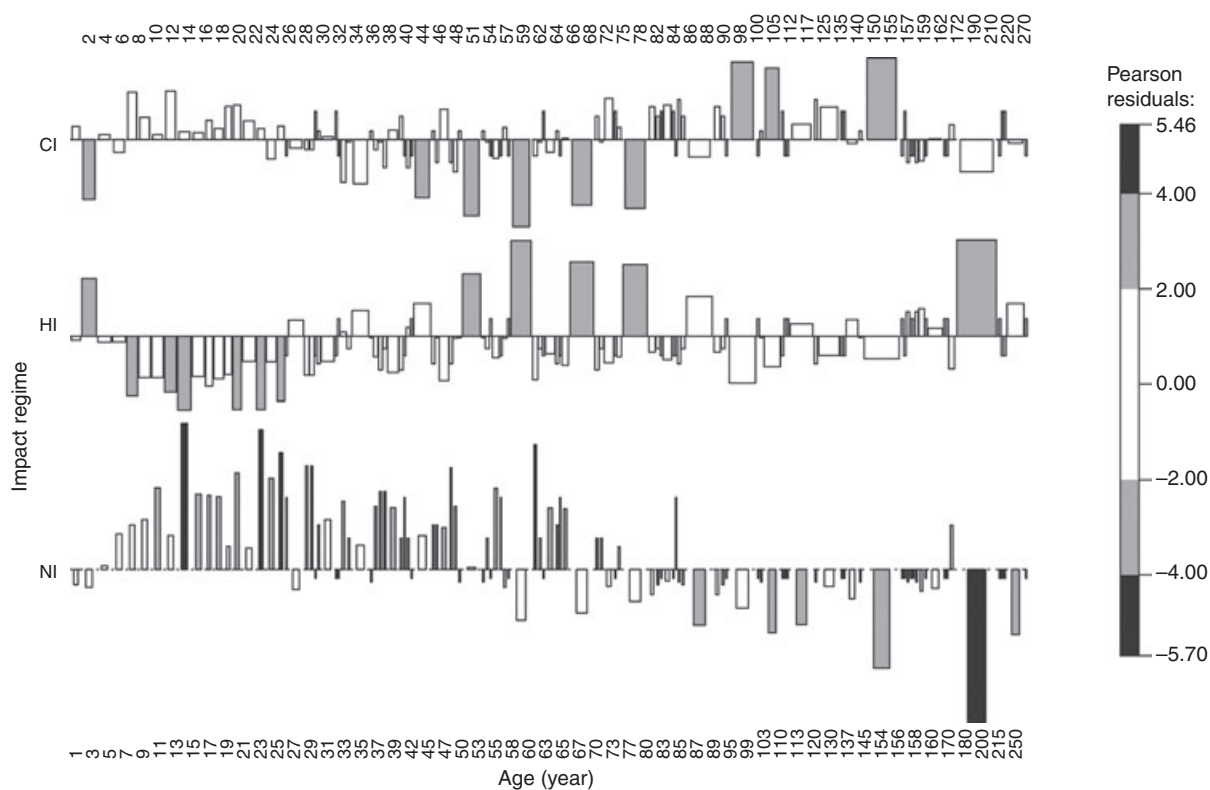
Fig 3 Association plot comparing the frequency of individuals of tree euphorbias of different ages in relation to megaherbivore impact regime. CI, contemporary impact, HI, historical impact, NI, no impact (steep slopes)
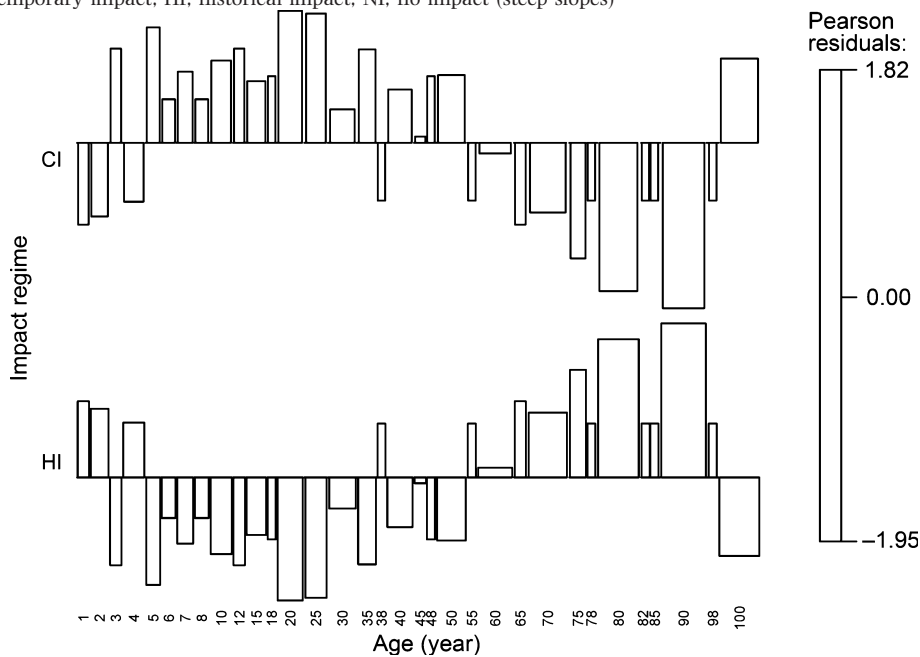

Fig 4 Association plot (truncated to ≤100 years) for moderate slopes comparing the frequency of individuals of tree euphorbias of different ages in relation to megaherbivore impact regime (CI, contemporary impact, HI, historical impact)

with tree aloes (*Aloe* spp.) – are the only canopy components of subtropical thicket that show strong levels of recruitment via genets. However, the remaining sites had low numbers of seedlings, indicating low levels of recruitment currently. The absence of seedlings could be caused by many factors acting individually or in synergy, such as local site characteristics (e.g. marginal sites for particular species), climatic variability producing episodic recruitment (as has been observed for other tree succulents (e.g. Jordan & Nobel, 1981), and browsing by small and medium-sized mammals (Midgley, 1993). We did not investigate these patterns further in our study. More demographic research using population projection matrices (Caswell, 1989) will be required to assess in detail the variation in, and factors influencing, population growth of tree euphorbias.

Contemporary megaherbivore impacts

Our data confirm the results of other studies which have shown that megaherbivore impacts on vulnerable plants decline with increasing terrain slope (Weyerhauser, 1985; Bond & Loffell, 2001, Heilmann *et al.*, 2006; Edkins *et al.*, 2007). While very steep slopes do appear to provide a refuge for tree euphorbias, these sites are atypical in that median ages are a half to a third that of plants on more level ground. We suspect that on these very steep slopes where soils are invariably skeletal, tree falls reduce the incidence of taller and older plants.

In megaherbivore-exposed sites on level and gentle terrain, both black rhinoceros and elephant targeted younger, and hence smaller, tree euphorbia individuals. This is consistent with observations by Heilmann *et al.* (2006) from two sites in our study area involving black rhinoceros and *E. tetragona* and *E. triangularis*. They observed the highest probability of rhino-induced mortality for individuals of between 2 and 5 m. In their study sites, this height class corresponds with the same age class (ca. 35–80 years) that was underrepresented in our sites that were subject to contemporary megaherbivore impacts (unpublished data). Heilmann *et al.* (2006) suggested that black rhinoceros target smaller individuals since these provide the same rewards (terminal branchlets of high water and nitrogen content) as larger individuals but require less effort to obtain. Weyerhaeuser (1985) and Edkins *et al.* (2007) have shown that elephants select the smaller size classes of the tree succulent *Adansonia digitata* (baobab).

Historical megaherbivore impacts

A plausible hypothesis for the historical coexistence in subtropical thicket of megaherbivores and plants vulnerable to their impacts – such as tree euphorbias, tree aloes, mistletoes and a host of succulent shrubs and bulbs (Johnson, Cowling and Phillipson, 1999) – is that these two elements were separated spatially: the plants grew on steep, rocky ground and megaherbivores browsed on gentle bottomlands. Data from several studies at Addo Elephant National Park, where population loss and even local extinction of vulnerable plants have been attributed to elephant impacts (Penzhorn, Robertse & Olivier, 1974; Midgley & Joubert, 1991; Moolman & Cowling, 1994; Lombard *et al.*, 2001), indicate that spatial coexistence – at least at the exceptionally high elephant densities in the park – is tenuous. Also, on the basis of current rhino impacts on *E. tetragona* and *E. triangularis*, Heilmann *et al.* (2006) predict local extinction of these plants within a decade, depending on site and species. Furthermore, habitat modelling of tree euphorbia distributions in our study area has shown that predicted distributions (or fundamental niches) are way smaller than actual distributions (or realized niches) (Kamineth, 2004); megaherbivores may well have played a role in producing these distribution patterns.

Our data, however, do indicate local coexistence historically of megaherbivores and tree euphorbias. The majority of sites that were impacted by megaherbivores historically (HI and CI sites) supported numerous tree euphorbia individuals that are likely to have coexisted with both rhinos and elephants prior to their extirpation in the mid 1800s. Furthermore, we showed that many sites had age distributions that bore a signal of historical impacts. Given the severe contemporary impacts of megaherbivores on tree succulents, it seems likely that megaherbivore populations were lower than those of today or impacts were intermittent, owing to animal movements. Our data suggest that tree euphorbia densities on gentle terrain were lower before megaherbivore extirpation than those of today. After extirpation, populations of tree euphorbias would have grown rapidly (see Fig. 2c for J-shaped population-age structures) so that these species (along with tree aloes) have now become an unnaturally common component of thicket on gentle terrain. Interestingly, the observant accounts of naturalists who traversed the Subtropical Thicket Biome in the late eighteenth and early nineteenth centuries suggest that dense populations of tree aloes and euphorbias were mainly restricted to steep valley slopes (Skead, 2008). Postextirpation population

relaxation of tree succulents is probably widespread in bottomland thickets. The extensive hybridization on bottomlands between populations of species of tree aloe that were once isolated is a testament to this relaxation (Botes, 2006).

In conclusion, our study suggests that megaherbivores and tree euphorbias coexisted historically in Eastern Cape subtropical thicket. However, under contemporary impacts, tree euphorbia populations are declining rapidly (Heilmann *et al.* 2006; personal observation) Managers should consider monitoring the population structure of these species in protected areas where they coexist with megaherbivores. In particular, it will be useful to explore whether tree euphorbia density and age structure can be used as a surrogate for impacts on other plant species of conservation concern that are threatened by megaherbivore impacts.

Acknowledgements

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