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A mismatch between germination requirements and environmental conditions: Niche conservatism in xeric subtropical thicket canopy species?

V. Wilman *, E.E. Campbell, A.J. Potts, R.M. Cowling

Department of Botany, Nelson Mandela Metropolitan University, P.O. Box 7700, Port Elizabeth 6031, South Africa

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ABSTRACT

Seedlings of woody canopy species in the xeric forms of subtropical thicket are rare. Here we argue that the low number of seedlings is a consequence of niche conservatism where thicket species have retained germination and seedling establishment requirements associated with their ancestral origins in the warm, wet forests of the early Cenozoic. We test this hypothesis by evaluating the germination success of 12 arid and valley thicket species – representing a range of growth forms and dispersal modes – using a factorial germination experiment that sought to simulate permanently moist and deeply-shaded conditions (i.e. a wet forest environment) and sparsely-shaded and intermittently dry conditions (i.e. open microsites during the rainy season) in contemporary thicket environments. Germination success was significantly higher under the more mesic soil-moisture conditions for all species except *Pappea capensis* and *Jatropha capensis*. These results suggest that germination of thicket species requires long periods of high soil moisture supporting the niche conservatism hypothesis.

1. Introduction

Seedlings of woody canopy species in the xeric forms of subtropical thicket (Vlok et al., 2003) are rare (La Cock, 1992; Midgley and Cowling, 1993; Kruger et al., 1997; Sigwela et al., 2009). Kruger et al. (1997) suggest that this is a consequence of the life history of thicket canopy species: these long-lived shrubs or low trees regenerate primarily by sprouting (Midgley and Cowling, 1993). Consequently, they are likely to produce fewer seedlings than species that are unable to sprout and regenerate mainly from seeds, owing to the trade-off between allocating resources to vegetative versus sexual reproduction.

Here we argue that the low numbers of seedlings of woody canopy species in xeric thicket is a consequence of their early Cenozoic rainforest origins (Cowling et al., 2005); in other words, an example of niche conservatism (Wiens and Graham, 2005) whereby thicket species have retained germination and seedling establishment requirements associated with their ancestral origins in the warm, wet forests of the Paleocene and Eocene (Willis and McElwain, 2002). Consistent with this hypothesis is that some thicket species also grow as tall trees in nearby forest environments and produce copious seedlings (Cowling et al., 1997; Kruger et al., 1997). Furthermore, when observed, thicket seedlings – irrespective of whether they are wind-, bird- or mammal-dispersed – are invariably associated with beneath-canopy microsites (La Cock, 1992; Sigwela et al., 2009). In comparison to open microsites, beneath-canopy ones are cool (Lechmere-Oertel et al., 2005) and extraordinarily rich in soil organic matter (Mills and Cowling, 2006, 2010; van der Vyver et al., 2013). Consequently, after a rainfall event, soil moisture levels are much higher beneath thicket canopies, and soil moisture persists for much longer than in open sites (van Luijk et al., 2013).

Almost no research has been conducted on the seed biology of thicket canopy species. Cowling et al. (1997) hypothesised that the organic-rich soils beneath dune thicket canopies (Cowling, 1984) would promote germination via some unspecified biological interaction. However, germination experiments in a nursery environment refuted this hypothesis: while germination of six thicket species was highest and occurred more rapidly under shaded conditions, soil type (organic versus mineral) had no effect (Cowling et al., 1997).

Here we test a prediction of the niche conservatism hypothesis by conducting germination trials on 12 arid and valley thicket species representing a range of growth forms and dispersal modes. We implemented a factorial germination experiment to simulate permanently moist and deeply-shaded conditions one would expect under a closed-canopy forest environment on the one hand, and sparsely-shaded and intermittently dry conditions one would expect in open microsites during the rainy season in contemporary thicket environments (van Luijk et al., 2013). We expected woody canopy species associated with ancient lineages to show highest germination and seedling survivorship in the high-shade, high-moisture treatment. Given that seed size is generally a good predictor of germination success and seedling survival (Harper, 1977; Jurado and Jurado, 1992; Moles and Westoby, 2006), we also assessed the effect of seed size on germination success.

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* Corresponding author. Tel.: +27 73 740 6278.
E-mail address: firevixen@live.co.za (V. Wilman).

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2. Methods

2.1. Study site and species

The study site is located between Cambria and Goedehoop within the Baviaanskloof Megareserve (33° 40′ 39.28″ S 24° 36′ 12.97″ E). We targeted species for seed collection from Gamtoos Valley Thicket and Baviaans Spekboom Thicket, both forms of Valley Thicket (Vlok et al., 2003). In its pristine state, Valley Thicket is a virtually impenetrable tangle of multi-stemmed low trees, shrubs and vines, which shade an understory of succulents and geophytes. Dominant species in both thicket forms are *Pappea capensis* and *Portulacaria afra*. Gamtoos Valley Thicket is characterised by a high abundance of *Schotia latifolia*, *Euphorbia triangularis* and the locally endemic *Cussonia gamtoosensis*; Baviaans Spekboom Thicket has a high abundance of *Aloe speciosa* and *Searsia longispina* (Vlok et al., 2003). Soils are clay-rich and fertile, and have a high oxidizable carbon content (Cowling, 1984). The climate of the study area and nursery (where the germination trials were conducted) is warm-temperate and semi-arid: extreme minimum temperatures are seldom below freezing while maxima occasionally exceed 40 °C; rainfall ranges from 350 to 550 mm yr^{-1} with peaks recorded in spring and autumn (Cowling, 1984).

Between November 2008 and October 2009 we collected seeds of 12 species from intact thicket, representing a range of thicket growth forms, dispersal modes and guilds (Table 1). Seeds were subsequently stored at room temperature at the Kouga Dam nursery, where germination trials were undertaken (see below). In order to avoid fungal infections during storage, and assuming thicket fruits would have been eaten before being dispersed, we removed the fruit pulp and seed coats where necessary (Hartmann et al., 2002; Cowling et al., 1997).

2.2. Germination trials

We conducted the germination trials in a Gamtoos Valley Thicket environment at the Kouga Dam nursery (33° 45′ 05.37″S 24° 35′ 08.28″ E), a facility established by the Department of Environment Affairs. Our experiments sought to simulate deeply shaded (as beneath dense thicket) versus sparsely shaded (as in open sites between thicket clumps) conditions, and permanently versus intermittently moist conditions, and combinations thereof. Given that shading and watering are difficult to vary over small spatial scales, the experimental design follows a split-plot design with two greenhouses having different shading regimes, and two different watering regimes implemented within each greenhouse. The shading treatments were as follows: 40% green shade-cloth with 40-UV block and additional mountain shading in the late afternoon (deep shade); 12% white shade-cloth with 30 UV-block and full day sun exposure (sparse shade). The moisture treatments were designed to simulate soil moisture conditions after a series of large rainfall events, when saturated moisture conditions are sustained for a long period, and conditions associated with sporadic rain, providing saturated conditions intermittently (van Luijk et al., 2013). We experimented with various watering regimes and settled on the following regime which provided the desired outcome: watering for 20 min at ca. 10h00 every day (permanently moist) and every second day (intermittently moist). Even during hot spells (the experiment was implemented in summer), the growing medium associated with the permanently moist treatment remained saturated.

As a planting medium, we used a mixture comprising 45% fine sand, 45% fine bark and 10% vermiculite. This mixture is likely to be relatively nutrient poor in comparison to the organic-rich soils of the thicket (Mills and Cowling, 2010); however, we used this relatively sterile and nutrient free soil because Cowling et al. (1997) found that using organic-rich soil harvested from under thicket clumps had no effect on germination success, and germination is generally not dependant on soil nutrients (Bewley and Black, 1985). In addition, using this mixture prevented pathogens and other organisms from influencing the experiment or contaminating the shade houses. We prepared a total of 960 seed trays (3200 seeds per species), consisting of 20 replicates of each treatment combination (moisture × shade). Each replicate consisted of a soil filled seed tray (34 × 37 cm) containing 40 seeds. Sowing took place continuously from the 22 October until 30 October 2009. Seeds were sown in eight rows of five and covered with the growing medium to approximately three times the seed diameter. Many thicket species have fleshy fruits that are dispersed by birds or mammals (Cowling, 1984), and the passage through the gut of an animal is often required for germination (Cowling, 1984). Hence, we sterilized and scarified – in 3% bleach (sodium hypochlorite) – the seeds of all species except for *Lycium ferocissimum* and *Aloe ferox* (Hartmann et al., 2002). *L. ferocissimum* and *A. ferox* were not treated as their seeds are small, delicate and lack a protective coat and, therefore, are likely to be damaged by the scarification.

Table 1
Characteristics of study species.

Species (family)	Growth form and guild (in valley thicket)	Fruit description and dispersal vector
Aloe ferox Mill. (Asphodelaceae)	Single stemmed, rosette leaf succulent (2–4 m) Open	3-lobed capsule; wind
Boscia oleoides (Burch. ex DC.) Toelken (Brassicaceae)	Tall, evergreen shrub to low tree (3–5 m) Canopy	Berry (13 mm); bird
Cussonia gamtoosensis Strey (Araliaceae)	Low, evergreen tree (4–5 m) Canopy	Drupe (8 mm); bird
Ehretia rigida (Thunb.) Druce. (Boraginaceae)	Tall, drought-deciduous shrub to low tree (3–5 m) Canopy margin	Berry (8 mm); bird
Euclea schimperi (A.DC.) Dandy (Ebenaceae)	Tall, evergreen shrub to low tree (3–5 m) Canopy	Berry (20 mm); bird
Grewia robusta Burch. (Malvaceae)	Tall, drought-deciduous shrub (2–3 m) Canopy	4-lobed drupe; bird
Jatropha capensis (L.F.) Sond. (Euphorbiaceae)	Stem-succulent, drought-deciduous shrub (2–3 m) Canopy margin	3-lobed capsule bearing dry seeds; explosive
Lycium ferocissimum Miers. (Solanaceae)	Tall, drought deciduous shrub (2–3 m) Canopy margin and open	Berry (6 mm); bird
Pappea capensis Eckl. & Zeyh. (Sapindaceae)	Tall, evergreen shrub to low tree (3–5 m) Canopy	3-lobed capsule bearing fleshy fruit (20 mm); bird
Sideroxylon inerme L. (Sapotaceae)	Tall evergreen shrub to low tree (5–8 m) Canopy	Berry (10 mm); bird
Searsia longispina (Eckl. & Zeyh.) Moffat (Anacardiaceae)	Tall, evergreen shrub to low tree (3–4 m) Canopy	Drupe (6 mm); bird
Schotia latifolia Jacq. (Fabaceae: Caesalpinoideae)	Tall, evergreen shrub to low tree (3–5 m) Canopy	Flattened pod (150 × 40 mm); mammal

After sowing, the trays were watered and sprayed with a fungicide (Proplant diluted at 1.5 ml/l water) and were placed inside the shade houses on benches approximately 1.5 m high made of treated poles strung with wire. The placement of trays (one species per tray), and therefore species, was randomised within each shade and water treatment combination block.

We counted the number of germinants at intervals of seven days for a period of nine weeks. Seedlings were considered to have germinated when cotyledons emerged above the soil surface. Wire pins were inserted into the trays to mark seedlings that had been counted, and also to record any mortality.

2.3. Statistical analysis

All germination results were converted to a percentage of the sown seeds per tray, while mortality results converted to a percentage of the number of germinated seeds per tray.

Germination values for combinations of shade and watering treatments (with and without species as an additional factor) were not normally distributed even after multiple attempts at transformation to conform to normality; therefore we used a permutation-based split-plot ANOVA (Anderson, 2001) using the 'lmPerm' package (Wheeler, 2010; 10,000 permutations or until the standard deviation of the estimated P-value fell below 0.005) in R version 2.15.1 (R Core Development Team, 2013). Note that we report significance levels using traditional F values (p-values) and using permutation tests (P-values). A two-factor split-plot ANOVA was used to compare germination (G) with the effects of shade (Sh; the whole plot treatment) and moisture regime (M; the subplot treatment) with tray placement (T) position treated as the blocking factor [G ~ Sh*M + Error(T/M) in R language]. In a similar manner, a three-factor split-plot ANOVA was conducted with species (Sp) included as a subsubplot treatment [G ~ Sh*M*Sp + Error(T/Sp/M)]. Further comparisons of germination between treatments and/or species were investigated using non-parametric tests (Kruskal–Wallis rank sum tests conducted in R); the 'pgirmess' library was used to conduct a post-hoc multiple comparison test after the Kruskal–Wallis analyses (Seigel and Castellan, 1988) — this determines which groups are significantly different ($\alpha = 0.05$) using adjusted pairwise comparisons.

3. Results

The two-factor split-plot ANOVA with the fixed effects of two levels for shading (12% and 40%) and moisture regime (intermittent and permanent) yielded main effects for both shade ($F_{1,\,888} = 102.8$, $p < 0.001$; $P < 0.001$) and moisture ($F_{1,\,956} = 11.0$, $p < 0.001$; $P < 0.001$) with increased germination under 40% shading or permanent moisture (Fig. 1). The interaction effect was also significant ($F_{1,\,954} = 30.14$, $p < 0.001$; $P < 0.001$); this was expected as both treatments play a role in determining soil moisture and thus plant water stress. The interaction effect indicates that the shading or moisture treatment effect was greater under permanent moisture and under 40% shading, as shown in Fig. 1 with additional non-parametric analyses. A three-factor split-plot ANOVA with the shading and moisture treatments plus 12 species yielded main effects for shade ($F_{1,\,888} = 408.9$, $p < 0.001$; $P < 0.001$), moisture ($F_{1,\,888} = 43.6$, $p < 0.001$) and species ($F_{11,888} = 43.3$, $p < 0.001$; $P < 0.001$). There were also significant interaction effects between moisture and shade ($F_{1,\,888} = 119.7$, $p < 0.001$; $P < 0.001$), moisture and species ($F_{11,\,888} = 2.84$, $p = 0.001$; $P = 0.002$; $P < 0.001$), shading and species ($F_{11,888} = 31.4$, $p < 0.001$) and amongst all three ($F_{11,888} = 19.6$, $p < 0.001$; $P < 0.001$).

It is unsurprising that there were significant interactions between all of the terms as germination success varied across species and there were different species-specific responses to the different treatments (Fig. 2). For example, the treatment combination with the greatest water stress (12% shading and intermittent moisture) generally had the lowest germination success, except for *P. capensis* (not significantly different from other treatments) and *Jatropha capensis* (significantly higher than all other treatments). Another example is that the other three treatment combinations (i.e. excluding 12% shading and intermittent moisture) did not deliver any significant differences in germination success within species, with two exceptions: *Ehretia rigida* and *Boscia oleoides*.

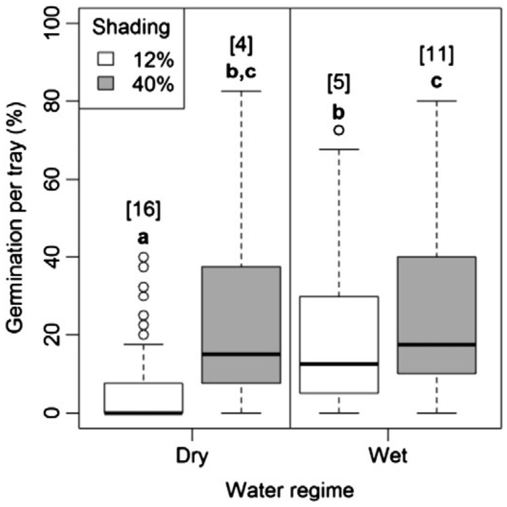

Fig. 1. Box and whisker plots of overall germination success for all 12 thicket species contrasting the effects of moisture and shade regimes (n = 240 per combination). Two moisture and shading regimes were used: dry = watering every two days; wet = daily watering; 12% or 40% shade-cloth. The percentage of seedling mortality after nine weeks is shown in brackets above each box and whisker plot in square brackets. Treatment combinations are statistically different (Kruskal–Wallis rank-sum test, $\chi^2 = 254$, df = 3, $p < 0.001$) and dissimilar superscripts are shown to denote significant differences between specific combinations at $p < 0.05$ (post-hoc multiple comparison test).

The percentage mortality of all seedlings was fairly low across species (<20%) except for *L. ferocissimum* that had an overall mortality of 59%. The percentage mortality varied across treatments within species, with high percentages often associated with low germination success. Mean seed weight was not correlated with overall germination, seedling mortality or seedling survival after nine weeks from planting (Fig. 3).

4. Discussion

Our results suggest that the paucity of seedlings of woody canopy species in xeric (arid and valley) thicket communities is because seed germination requires long periods of high soil moisture, something that is rare in the semi-arid environments of the subtropical thicket biome (La Cock, 1992; van der Vyver et al., 2013; van Luijk et al., 2013). One would expect that perennial plants of semi-arid environments would exhibit an array of germination and seedling establishment strategies that are geared to drought evasion or avoidance. Two of our species did show germination cues better suited than the others to semi-arid environments, namely *P. capensis* and *J. capensis*. *P. capensis* is a common canopy tree of xeric thicket and can persist in the driest forms (Vlok et al., 2003); despite the low germination success we observed, its seedlings are the most commonly encountered in intact and degraded xeric thicket (Midgley and Cowling, 1993; Sigwela et al., 2009; van der Vyver et al., 2013). This species has been reported to have physical and physiological seed dormancy by Kew's "Difficult" Seeds Project (Royal Botanic Gardens, 2013), suggesting that germination rates may have been higher had the experiment run for longer or with targeted germination cues for this species. *J. capensis* grows on the margins of thicket clumps and is not dispersed by birds; consequently, it may be adapted to germination in open sites where moisture conditions are harsher than beneath thicket clumps (van Luijk et al.,

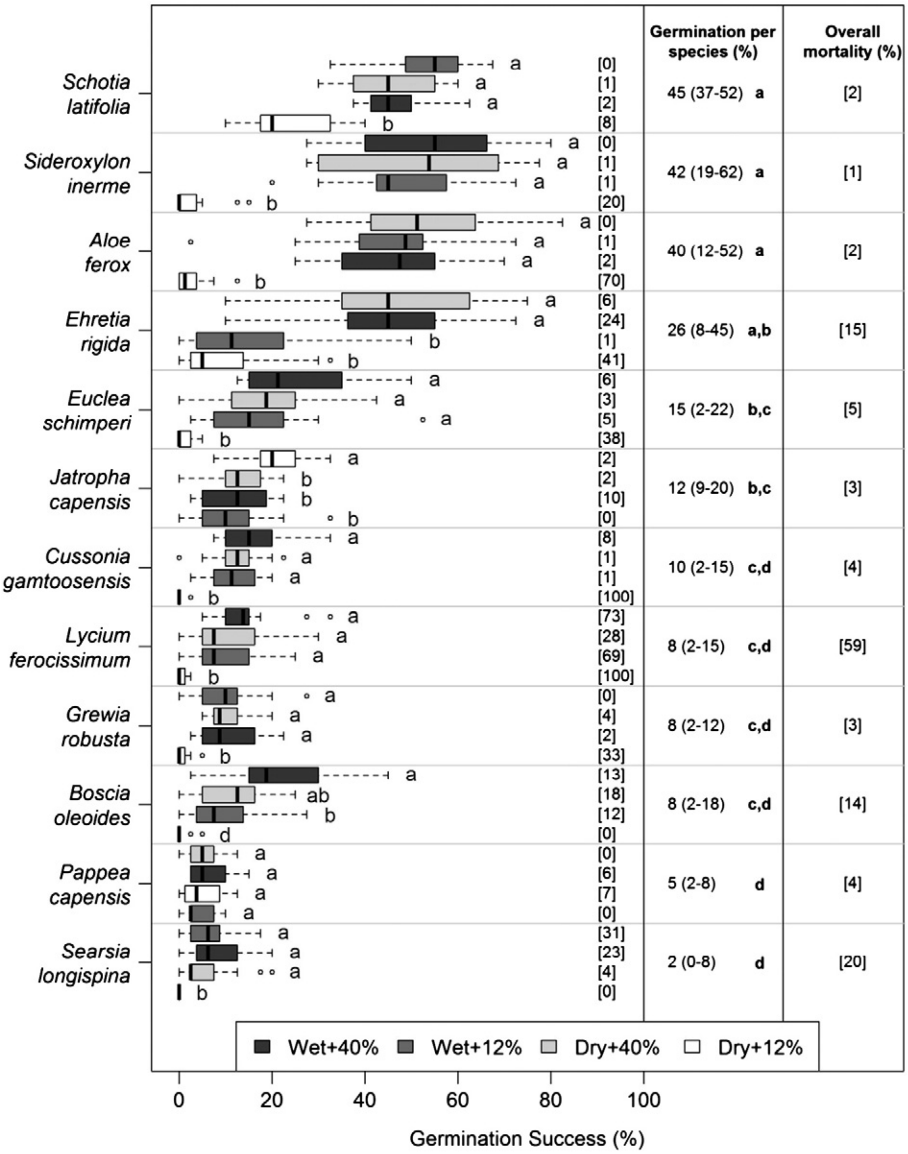

Fig. 2. Box and whisker plots of germination success (% per tray) for all treatment combinations for each thicket species. The germination success within each species is ordered from highest to lowest median values per treatment combination. All treatment combinations per species, except for *Pappea capensis*, showed significant differences between treatments (Kruskal–Wallis rank sum test, df = 3, $p < 0.01$) and dissimilar superscripts within species denote significant differences between treatment combinations at $\alpha < 0.05$ (post-hoc multiple comparison test). The median (25th and 75th percentiles) of the germination success within species across all treatments is shown; the germination success between species is significantly different (Kruskal–Wallis rank-sum test, $\chi^2 = 342$, df = 11, $p < 0.001$) and significant differences between species follow the same superscript convention as used above. The percentage of overall mortality after nine weeks per species – within or across treatments – is shown in square brackets.

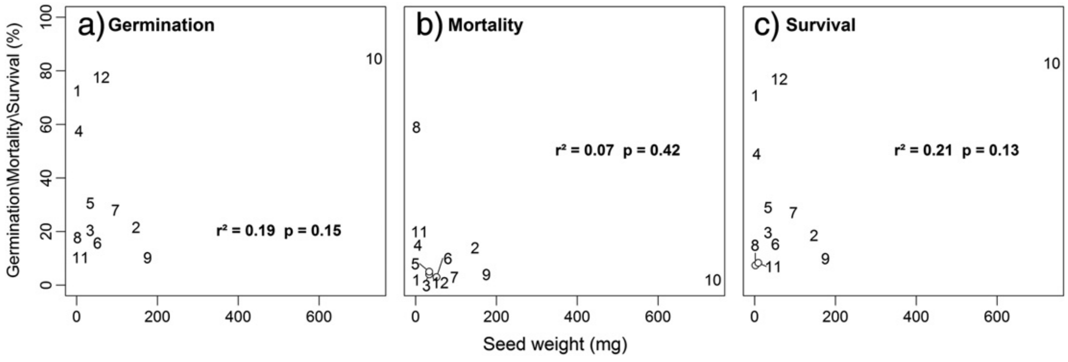

Fig. 3. Mean seed weight versus (a) the total germination of all seeds across all treatments, (b) the seedling mortality post-germination after nine weeks from planting, and (c) the total seedling survival after nine weeks. Species are: 1: *Aloe ferox*; 2: *Boscia oleoides*; 3: *Cussonia gamtoosensis*; 4: *Ehretia rigida*; 5: *Euclea schimperi*; 6: *Grewia robusta*; 7: *Jatropha capensis*; 8: *Lycium ferocissimum*; 9: *Pappea capensis*; 10: *Schotia latifolia*; 11: *Searsia longispina*; 12: *Sideroxylon inerme*.

2013). However, *A. ferox*, another non-canopy species that recruits seedlings in open sites (RMC, pers. obs.), had uniformly and relatively high germination under all treatments except the low-shade, intermittent moisture one. *L. ferocissimum*, a shrub of thicket margins and open sites that increases in abundance with grazing-induced degradation, also showed significantly lower germination under the most water-stressed treatment. This species also had amongst the lowest germination success and the highest seedling mortality. Clearly, its colonizing ability must have more to do with seed numbers than quality. Interestingly, contrary to evidence for perennial plants from semi-arid environments (Gutterman, 1993; Jurado and Jurado, 1992; Moles and Westoby, 2006), seed size was a poor predictor of germination success and seedling mortality or survival amongst our study species.

We suggest that the high moisture demand for germination of thicket canopy shrubs is a legacy of the early Cenozoic rainforest origins (Cowling et al., 2005). This germination niche has been conserved (sensu Wiens and Graham, 2005; Wiens et al., 2010), because it has not been maladaptive in the drier environments of the Neogene: thicket species are long-lived and can reproduce via ramets (Midgley and Cowling, 1993), thus sexual reproduction is not a requirement to maintain populations over decade- or even century-long periods (Midgley and Cowling, 1993). However, occasional sexual recruitment is necessary to maintain populations in the longer term and to expand populations to distant sites in the face of Pleistocene climate change (Potts et al., 2013). Rare episodes of more-frequent-than-usual rainfall would enable germination of seedling in beneath-canopy microsites where high organic matter and relatively cool conditions would ensure the retention of soil moisture between gaps in rainfall events (van Luijk et al., 2013). Under even more exceptional rainfall circumstances, thicket seedlings may also germinate and survive in more open microsites. However, surveys show that the vast majority of seedlings in xeric thicket are associated with beneath-canopy microsites (La Cock, 1992; Sigwela et al., 2009).

Interestingly, thicket species growing in the winter-rainfall region of South Africa showed much lower resistance to water stress and higher water use efficiency than co-existing fynbos and karroid shrubs (Pratt et al., 2012). These features were attributed by Pratt et al. (2012) to the life history characteristics of the thicket species: obligate resprouting with occasional seedling establishment in the relatively mesic microsite beneath the thicket canopy. This life history is also well represented in the Mediterranean-climate vegetation of the Mediterranean Basin, California and Chile and the component species also have their origins in rainforest floras of the early Cenozoic (Keeley et al., 2012). The water-demanding, and other, attributes of these species that appear “non-adaptive” in the current environmental regime have – like their thicket counterparts – been attributed to niche conservatism (Ackerly, 2004; Herrera, 1992).

Kruger et al. (1997) observed a positive correlation between seedling abundance and canopy height of thicket and forest vegetation in and adjacent to the thicket biome, which they interpreted as a trade-off between vegetative reproduction (prevalent in low-canopy thicket) and sexual reproduction (prevalent in tall-canopy forest). However, our niche conservation hypothesis could equally explain this pattern given that the gradient in increasing canopy height mirrors a gradient from semi-arid to humid rainfall regimes (Cowling and Campbell, 1983). Kruger et al.'s (1997) hypothesis predicts that species common to both thicket and forest environments – of which there are many (Vlok et al., 2003) – should produce fewer and lower quality seeds per area of canopy when growing as sprouting thicket plants than as reseeding forest plants. Unfortunately, data are lacking to test this hypothesis. However, fruit production of xeric thicket woody canopy species can actually be quite high, albeit highly variable: mean (SD) values recorded over one year per 2500 cm^2 of canopy for *Euclea undulata*, *P. capensis* and *S. longispina* are 1695.3 (2235.0), 78 (130.8), and 394.7 (650.9), respectively (Sigwela et al., 2009). Furthermore, germination success and seedling survival – and hence, seed quality – was high under the least water-stressed treatment for several canopy shrubs in our sample.

Finally, our results have some implications for the restoration of degraded thicket for earning carbon credits via the planting of truncheons of the leaf succulent canopy tree *P. afra*, a project currently being implemented on a wide scale in the thicket biome by the South African Government (van der Vyver et al., 2012). Van der Vyver et al. (2012) reported that other than *P. afra*, which showed no mortality, transplanted propagules of canopy species had almost zero survival in field trials, even when planted amongst restored 30-year *P. afra* plants. We suspect that low tolerance to stress of the woody canopy species is another manifestation of niche conservatism. We concur with van der Vyver et al. (2012, 2013) that restoration of woody canopy species, either using seeds or seedlings, is fruitless; instead, restoration practitioners should rely on the spontaneous restoration, likely associated with rare series of rainfall events, of populations of wood canopy species that has been observed, along with pre-disturbance carbon storage, in sites restored with truncheons of *P. afra* for 40 years (van der Vyver et al., 2013).

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