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Spontaneous Return of Biodiversity in Restored Subtropical Thicket: *Portulacaria afra* as an Ecosystem Engineer

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Abstract

An accepted criterion for measuring the success of ecosystem restoration is the return of biodiversity relative to intact reference ecosystems. The emerging global carbon economy has made landscape-scale restoration of severely degraded *Portulacaria afra* (spekboom)-dominated subtropical thicket, by planting multiple rows of spekboom truncheons, a viable land-use option. Although large amounts of carbon are sequestered when planting a monoculture of spekboom, it is unknown whether this is associated with the return of other thicket biodiversity components. We used available carbon stock data from degraded, restored, and intact stands at one site, and sampled carbon stocks at restored stands at another site in the same plant community. We also sampled plant community composition at both sites. The total carbon stock of the oldest (50 years) post-restoration stand (250.8 ± 14 t C ha^{-1}) approximated that of intact stands (245 t C ha^{-1}) and we observed a general increase in carbon content with restoration age (71.4 ± 24 t C ha^{-1} after 35 and 167.9 ± 20 t C ha^{-1} after 50 years). A multiple correspondence analysis separated degraded stands from stands under restoration based on ground cover, floristic composition, and total carbon stock. Older post-restoration and intact stands were clustered according to woody canopy recruit abundance. Our results suggest that spekboom is an ecosystem engineer that promotes spontaneous return of canopy species and other components of thicket biodiversity. The spekboom canopy creates a cooler micro-climate and a dense litter layer, both likely to favor the recruitment of other canopy species.

Key words: abiotic threshold, alternative stable states, carbon sequestration, ecosystem carbon stocks, post-restoration recruitment, spekboom.

Introduction

The attributes defining a restored ecosystem should include some measure of the return of species composition, ecosystem services, and ecological functioning (SERI 2004; Hobbs 2007; Benayas et al. 2009). Carbon sequestration projects, where trees are planted to earn carbon credits, should aim to provide investors with the benefit of both carbon and biodiversity credits (Bekessy & Wintle 2008). This requires confirmation of the restoration of a suite of species, representing different functional groups present in a reference intact system, via active or spontaneous return (White & Walker 1997; Herath et al. 2009).

Here we focus on the restoration of endemic-rich South African subtropical succulent thicket (Vlok et al. 2003; Cowling et al. 2005) for carbon credits (Mills et al. 2007, 2009). Component woody canopy (2–5 m) plants, e.g. *Euclea undulata, Pappea capensis* and *Schotia afra* are long-lived and reproduce mainly via ramets, or occasionally via seedlings that originate mostly from vertebrate-dispersed propagules (Midgley & Cowling 1993; Sigwela et al. 2009). While relatively resilient to browsing by indigenous herbivores (Stuart-Hill 1992), subtropical thicket is highly vulnerable to browsing by domestic goats. Sustained, heavy browsing can transform the dense closed-canopy thicket into an open community comprising scattered and degraded thicket clumps and isolated trees in a matrix of ephemeral herbs (Lechmere-Oertel et al. 2005*a*, 2005*b*). Particularly, vulnerable are drier (<450 mm/year) forms of thicket (Arid and Valley forms) (Vlok et al. 2003) dominated by the tree-like leaf succulent, *Portulacaria afra* (hereafter spekboom) (Stuart-Hill 1992; Lechmere-Oertel et al. 2005*a*, 2005*b*). Of the 16,942 km^2 of solid (unbroken canopy) spekboom-dominated thicket, 46% has been heavily, and 36% moderately degraded (Lloyd et al. 2002). Spekboom is the first canopy dominant to succumb to browsing, being entirely eliminated in severe cases of degradation.

Spontaneous recovery of canopy species populations does not occur in browsing-degraded spekboom thicket, even decades after the cessation of goat-browsing (Lechmere-Oertel et al. 2005*a*; Sigwela et al. 2009). Recruits of canopy species—both ramets and genets—are invariably associated

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with the rich layer of organic mulch that accumulates beneath the intact thicket canopy (Sigwela et al. 2009). Heavy goat browsing alters the beneath-canopy microclimate and destroys the rich layer of organic mulch (Lechmere-Oertel et al. 2008). Deprived of an organic carbon-rich soil, and subject to ongoing browsing, adult canopy plants eventually die, thicket clumps steadily dwindle (Lechmere-Oertel et al. 2005*a*), and recruitment fails (Sigwela et al. 2009). The ecosystem is locked into a degradation trajectory that can only be reversed by active restoration such that the abiotic threshold imposed by changes in soil properties and microclimate is transcended (Briske et al. 2006).

The recent emergence of the global carbon economy has provided an unprecedented opportunity to finance the restoration of degraded thicket via carbon credits (Galatowitsch 2009). Spekboom-dominated ecosystems store carbon in excess of 200 t/ha, a remarkable feature for a xeric ecosystem and comparable to that of mesic forest ecosystems (Mills et al. 2005*a*). Spekboom contributes most of the above-ground carbon (Mills & Cowling 2006; Lechmere-Oertel et al. 2008) and, with its dense canopy, provides the relatively cool and dry conditions necessary for the accumulation of large levels of soil carbon (Lechmere-Oertel et al. 2005*a*, 2005*b*; Cowling & Mills 2010). Comparisons of degraded and intact stands reveal carbon losses of more than 80 t C ha^{-1} (Mills et al. 2005*b*). These losses are evident from the decrease in above ground biomass, but are also a result of the reduction in soil organic carbon stock (Mills & Fey 2004).

Using the opportunity provided by a long-standing (1976–1998) spekboom restoration trial implemented by a landowner, Mills & Cowling (2006) found that 112 t C ha^{-1}, at a rate of 4.2 t/year, was sequestered in this 27-year period. These data provided the impetus for the South African government to fund spekboom restoration research and implementation at the landscape level. This initiative, the Subtropical Thicket Restoration Project (STRP), has the broad aim of creating an employment-intensive restoration economy funded by the carbon market (Mills et al. 2009). The current cost-effective methodology for restoration comprises the planting of spekboom truncheons (height: 250–650 mm; stem diameter: 15–35 mm) at 1–2 m spacing in parallel rows; the truncheons are sourced from surrounding relatively intact areas (Mills et al. 2007). Spekboom establishes readily from truncheons, which can be inexpensively harvested.

Van der Vyver et al. (2012) demonstrated that active restoration of woody canopy species other than spekboom was neither economically nor ecologically feasible. The question then arises: does the planting of spekboom monocultures facilitate the spontaneous restoration of other thicket species, especially woody canopy ones? The degradation dynamics of spekboom thicket are consistent with state-and-transition models (Milton & Hoffman 1994). We hypothesize that using spekboom as the focal species for restoration will achieve carbon sequestration goals and ensure that thresholds constraining the return of biodiversity are overcome (Briske et al. 2006). Here we test this hypothesis by examining total carbon stock and plant species composition within different post-restoration age stands, and compare them with intact and degraded sites.

Methods

Site Description

We located two sites where spekboom truncheons were planted at various intervals over the past 50 years (Supporting Information Figs. S1–S4). The first site (Krompoort) was used by Mills and Cowling (2006) to estimate carbon sequestered by spekboom restoration. The site vegetation is a form of Arid Thicket (Sundays spekboomveld) (Vlok et al. 2003) and is extensively degraded. It is located on a gentle north-facing slope 320–400 m above sea level, with a mean annual precipitation of 317 mm (measured between 1970 and 2009) peaking in autumn and spring. Between 1976 and 1998, the Krompoort landowner planted spekboom cuttings in degraded thicket at regular intervals. Cuttings were planted in rows spaced 4.1–1.5 m apart, with the spacing between plants ranging from 0.8 to 1.1 m. Cuttings for most of the older plantings were sourced from a mountainous site circa 90 km to the northwest of Krompoort. This spekboom phenotype has an upright growth form and tends not to develop a “skirt” at ground level, a feature of most other forms. To provide a range of post-restoration ages, we selected the youngest stand (11 years), an intermediate stand (19 years) and the oldest stand (33 years) (all dates as of 2009). We selected an intact (closed-canopy thicket with spekboom as dominant component) and a degraded (an open pseudo-savanna with sparsely scattered trees and shrubs with an ephemeral grass and herb layer) area in close proximity to the restoration treatments, to act as reference and control stands, respectively.

The second study site (Rhinosterhoek) is situated approximately 25 km to the northwest of Krompoort. Rhinosterhoek has a similar altitude and aspect, and falls within the same vegetation type as Krompoort and also has neocalcic soils (WRB classification), belonging to the Cumulic subgroup (FAO 1998). These soils are derived from underlying shales, sandstones, and siltstones of the Bokkeveld Group. Rhinosterhoek receives a mean annual precipitation of 265 mm (measured between 1950 and 2008). One row of truncheons was planted in degraded thicket, approximately 40 m long, on a gentle slope behind the farmhouse, perpendicular to the slope. Visibility of the spekboom row on a 1960 photograph provides proof that the row is at least 50 years old. In the mid 1970s, more cuttings were planted in adjacent rows in front of the older row (W. Rudman 2009, private landowner of the farm Rhinosterhoek, personal communication), and estimated to be approximately 35 years old. We also selected degraded and intact stands on nearby gentle, north-facing slopes. The Rhinosterhoek site has been protected from domestic goat browsing by a 2-m fence. Krompoort, also permanently enclosed, has been exposed to some goat-browsing for a few days annually during shearing time. Another difference was patch size. The 50-year (4.5 × 45 m) and 35-year (10 × 45 m) stands at Rhinosterhoek combined approximated the size of a single restored site at Krompoort. The 50-year stand comprised only one row of planted cuttings.

Our study system comprises "snapshot" experiments, and our experimental design, by lacking true replication of the variously aged restored stands, is pseudoreplicated (Hurlbert 1984).

However, for convenience, hereafter we refer to the intact, degraded, and variously restored stands as treatments.

Data Collection

Carbon. For Krompoort, we used Mills and Cowling's (2006) data to provide us with measures of the above- and belowground carbon content of the different-aged restoration blocks (Restored11, Restored19, Restored33) as well as a degraded stand (Degraded). To account for the difference between initial (2003) and the current sampling (October to November 2009), we adjusted carbon content upwards, using sequestration rates of 4.2 t C ha^{-1} yr^{-1} for Restored11, 2.7 t C ha^{-1} yr^{-1} for Restored19 and 4.1 t C ha^{-1} yr^{-1} for Restored33 stands (Mills & Cowling 2006). Mills and Cowling (2006) reported belowground carbon up to a depth of 1.0 m with varying sample intervals, whereas we recorded it to 0.6 m (see below). We assumed a negligible difference between our results and these values at 0.5-m depth in our comparisons of the two data sets.

We sampled total carbon stock at Rhinosterhoek on the 35-year-old (Restored35) and the 50-year-old (Restored50) restored stands, and in the nearby degraded area, using the procedures standardized for the STRP (Mills & Cowling 2010). For the belowground assessment, we excavated successive soil depth intervals, each 20 cm deep, up to a total depth of 60 cm (bedrock prevented deeper excavation at most localities). We sampled seven localities at each stand. Owing to the presence of bedrock we were able to extract soil samples at 40–60 cm depth from only six localities in Degraded and four in Restored35. Within each 20 cm depth interval three horizontally adjacent samples of soil (20 × 10 × 10 cm each) were excavated after all litter had been carefully removed. Following Mills and Cowling (2010), each of these samples was bagged, and the excavated cube was filled with preweighed river sand of known bulk density. After all samples (three per depth interval) were air-dried, they were weighed and sieved (<2 mm); one of these sieved soil samples was sent to a laboratory for analysis of carbon content using the Walkley–Black method (Walkley 1947); another was used to determine the total weight and wet-sieved to determine volume of rock within the sample; and another was used to extract the total root biomass. Extracted root fragments were weighed and dried in an oven at 60°C until constant mass. Carbon content of root biomass was calculated by multiplying dry material mass by 0.48 (Lamlom & Savidge 2003).

We sampled the litter component of aboveground carbon by collecting all litter in a 25 × 25-cm frame at seven localities in each of the stands, and then drying samples in an oven at 60°C until constant mass. We estimated the carbon content of above-ground biomass using species-specific allometric equations developed by Powell (2009). Depending on the species measured, either the canopy area or cumulative basal stem diameter was used as the determining variable. Following Powell (2009), for those species lacking allometric equations, we used equations of species of similar growth form and functional traits. We tested for significant differences between the different carbon components in sites of different restoration status using one-way analysis of variance (ANOVA) and Tukey's range test. The analyses were performed using R (R Development Core Team, 2010).

Table 1. Importance value scale showing categories allocated for adults (cover) and recruits (number of individuals) in sample quadrats.

Scale	*Adult plants (cover) (%)*	*Recruits (No. of individuals)*
1	0–2	1
2	2–5	2–5
3	5–10	6–10
4	10–25	11–15
5	25–50	16–25
6	50–75	26–34
7	75–100	35+

We used Mills et al.'s (2005*a*) data for carbon content of intact thicket. Using both allometric and direct sampling methods, their estimates of soil carbon to a depth of 50 cm were made using soil carbon concentrations and bulk density. They sampled eight stands in intact Sundays spekboomveld (Vlok et al. 2003) in areas located between Krompoort and Rhinosterhoek.

Community Structure. We randomly located ten 3 × 3-m quadrats in the different spekboom post-restoration stands (Restored11, Restored19, Restored33, Restored35) and in the adjacent intact and degraded stands at Krompoort and Rhinosterhoek. Owing to limited area suitable for sampling, we could only locate seven quadrats in Restored50. We estimated the cover and height of each species rooted within and overlapping the quadrat according to an arbitrary 7-point scale (Table 1). We identified as recruits (ramets and genets) of all individuals of woody, principally canopy species with a height equal or lower than 1 m (Midgley & Cowling 1993). Recruits were identified as pseudo-species (i.e. distinct from con-specific adults) and allocated to a category of the 7-point scale based on their abundance (Table 1). We assigned bare ground a cover value according to the scheme used for adult plants. Sampling was conducted in August to October 2009.

We used a generalization of multiple correspondence analysis (homogeneity analysis), to assess the relationships between different community structural attributes and composition. This multivariate method takes account of different types of variables, and allows one to visualize relationships between variables and their categories by jointly mapping samples and variables onto a shared metric plane. The analysis was performed using the R package homals (De Leeuw & Mair 2009). The results were plotted with the ade4 package (Chessel et al. 2004).

Table 2. Mean (SE) carbon stock (t/ha) of different ecosystem components, and rate of carbon sequestration (t ha^{-1} yr^{-1}) at Rhinosterhoek.

	Belowground C				*Aboveground C*					
Treatment	*Soil*	*Root*	*Total*	*n*	*Biomass*	*Litter*	*Total*	*n*	*Total*	*Rate*
Degraded	73.1 (11.0)	0.4 (0.09)	73.5 (11.0)	6	15.9^{a} (9.8)	0.0^{a} (0.01)	15.9^{a} (9.8)	7	82.9^{a} (14.7)	—
Restored35	96.7 (24.2)	4.1 (1.5)	100.8 (22.7)	4	45.4^{b} (10.6)	12.8^{b} (2.4)	58.2^{b} (10.9)	7	154.4^{b} (19.6)	2.0
Restored50	100.5 (11.8)	17.3 (10.4)	117.9 (9.4)	7	107.6^{c} (10.8)	25.3^{c} (2.2)	132.9^{c} (11.0)	7	250.8^{c} (14.0)	3.2
$F_{[2,14]}$-ratio	1.14^{NS}	1.57^{NS}	3.32^{NS}		20.33***	44.97***	31.44***		33.43***	

Belowground carbon is at 0–60 cm depth. Significance levels for one-way ANOVA are as follows: NS, non significant; ***$p < 0.001$. Values with different superscripts are significantly different ($p < 0.05$, Tukey's range test), SEs are in brackets. See Mills and Cowling (2006), Mills et al. (2005*a*), and Fig. 1 for data from Krompoort.

Within our context, where restoration treatment is expected to significantly change community composition over time, the rate of species turnover (β-diversity) provides a suitable comparative metric between treatments (See Appendix S5 for detailed motivation). Therefore, to assess the relationship between restoration status and diversity, we calculated α-, β- (multiplicative), and γ-diversity using Rao's (1982; Pavoine et al. 2005) quadratic entropy (a generalization of Simpson's index), following the methods outlined in de Bello et al. (2010). Indices were converted to Hill numbers (true diversity sensu Jost 2007), again following de Bello et al. (2010), and phylogeny was taken into account. We summarize the rate of turnover (Whittaker's multiplicative beta-diversity minus 1) using the first two dimensions of a principal coordinate analysis of the pairwise rate of turnover.

Results

Carbon

Predictably, carbon stocks increased significantly (3-fold in the case of Restored50) with increasing post-restoration age at Rhinosterhoek (Table 2). This increase was largely due to the aboveground component. Although there was a trend for soil and root carbon to increase with post-restoration age, differences were not significant.

Assuming that the spekboom-restored stands resembled the current degraded state prior to restoration, total (above- and belowground) carbon sequestration amounted to 167.9 t C ha^{-1} after 50 years and 71.4 t C ha^{-1} after 35 years. Of this, aboveground sequestration was responsible for 70% of Restored50 and 59% of Restored35. Annual sequestration rates amounted to 2.0 t ha^{-1} yr^{-1} after 35 years and 3.6 t ha^{-1} yr^{-1} after 50 years.

Combining the Rhinosterhoek (Table 2) and Krompoort (Mills & Cowling 2006; Mills et al. 2005*a*) data sets, there was a clear trend of increasing total carbon stock with increasing post-restoration age (Fig. 1). This pattern was stronger for aboveground than belowground carbon. Most noticeable was a spike in aboveground carbon in Restored50 and in soil carbon in Restored33. Total carbon stock of this treatment was similar to intact spekboomveld, although the proportion associated with soil carbon was smaller.

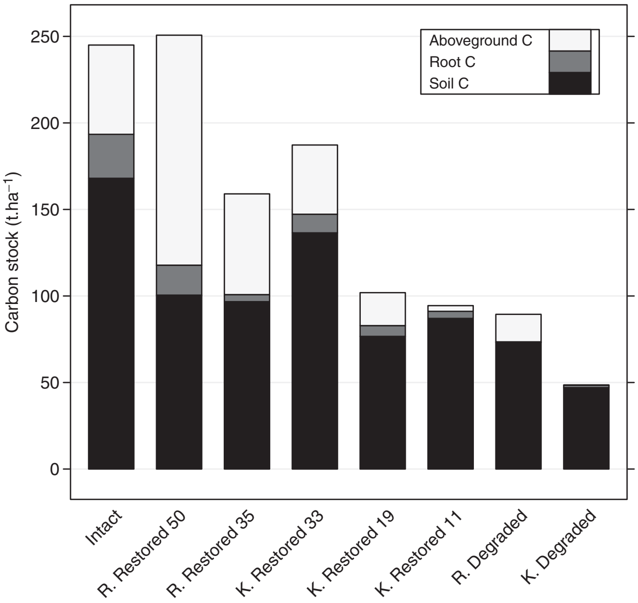

Figure 1. Carbon content of different components at Rhinosterhoek (measured at a soil depth of 60 cm), Krompoort and at Intact sites in the vicinity between the two sites (measured at a soil depth of 50 cm). Data for the Krompoort (prefix = K.) stands are from Mills and Cowling (2006) and data for the intact sites are from Mills et al. (2005*a*). Rhinosterhoek (prefix = R.) data from this study.

Community Structure

The multiple correspondence analyses showed a gradient in community structure, aligned along the horizontal axis of the ordination, in relation to restoration status at both Krompoort and Rhinosterhoek (Fig. 2). Generally, this gradient was associated with decreasing bare ground cover, increasing cover of canopy species (especially recruits), including spekboom, the restored species, and increasing total carbon stock. At both sites, the vertical axis appears to be related principally to canopy species recruit abundance. The abundance of recruits of canopy species at Krompoort was relatively low in the restored stands: of all recruits recorded, only 3, 3, and 1% were observed in the Restored11, Restored19, Restored33 treatments, respectively. The corresponding figure for the intact treatment was 15%. This is reflected in the strong clustering of the restored stands at the bottom end of the gradient, largely

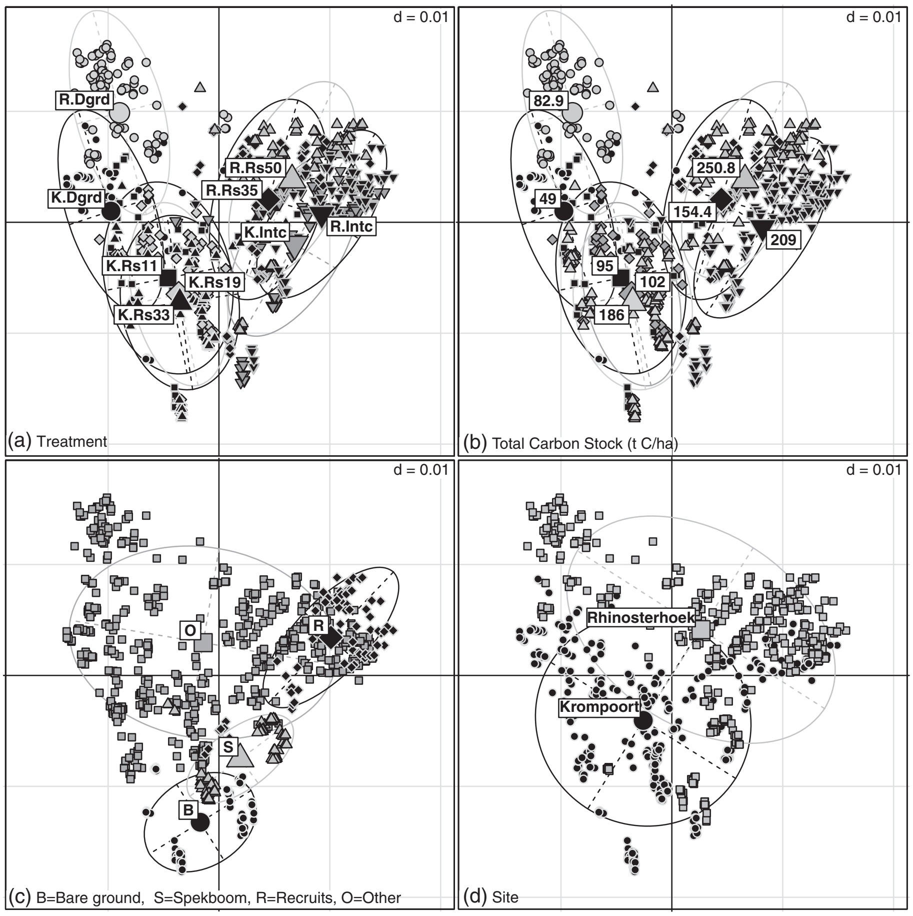

Figure 2. Multiple correspondence analysis of community structure data of two sites, Rhinosterhoek and Krompoort, each with stands of varying restoration status—in relation to (a) restoration treatment, (b) mean total carbon stock (t C ha^{-1}) per treatment, (c) specific community structure components such as bare ground (B), Spekboom cover (S), woody canopy recruits (R), and other (O) and (d) the two sampling sites. Small points are individual rows (entries) in our data matrix, large points indicate the origin of the different groupings shown in the labels. Ellipses encapsulate 67% of the data points associated with each point-cloud and their axes show the principle axes of variation (Chessel et al. 2004). "Rs" refers to restored stands and the number attached to number of years under restoration treatment. Prefix "K." denotes Krompoort stands and "R." Rhinosterhoek stands. "Dgrd" and "Intc" refer to Degraded and Intact stands, respectively.

separate from the intact stand. At Rhinosterhoek, Restored50 (49% of recorded recruits) occupies the top of the gradient, Restored35 (7% of recruits) the bottom, while the intact stands (21% of recruits) occupies a position intermediate between them.

A total of 172 recruits, belonging to 13 species, were recorded across all treatments (Fig. 3). Of these, 92% were found in Restored35, Restored50, and the two intact treatments. With the exception of *Rhigozum obovatum* and *Crassula ovata*, which are inter-canopy or canopy-margin shrubs, all of the recruits belong to canopy plants common in Sundays spekboomveld. The highest number of recruits was recorded for *Pappea capensis*, which, along with spekboom, is a regionally dominant tree.

Phylogenetic-based α-diversity increased monotonically with post-restoration time, as did rate of turnover (multiplicative beta-diversity minus 1), with the highest rate of turnover being between degraded and intact stands (see Appendix S6). The first two dimensions of a principal coordinate analysis of the rate of turnover (Fig. 4) show primarily an increase in species turnover with improving restoration status. The primary dimension (x-axis) is roughly twice as important (56.8%) as the second dimension or y-axis (21.6%). On the primary axis, the older restored sites converge with the intact sites, and this is also reflected in the increase in phylogenetic α-diversity (species richness) generally following the same pattern. The secondary axis shows some distance (vertical) between the two degraded stands, and between the older restored stands (35 and 50 years) and the intact sites, implying local site-based floristic differences.

Discussion

Our results show that total carbon stock in restored treatments increased with increasing post-restoration age, approximating that of intact spekboomveld 50 years post-restoration. We

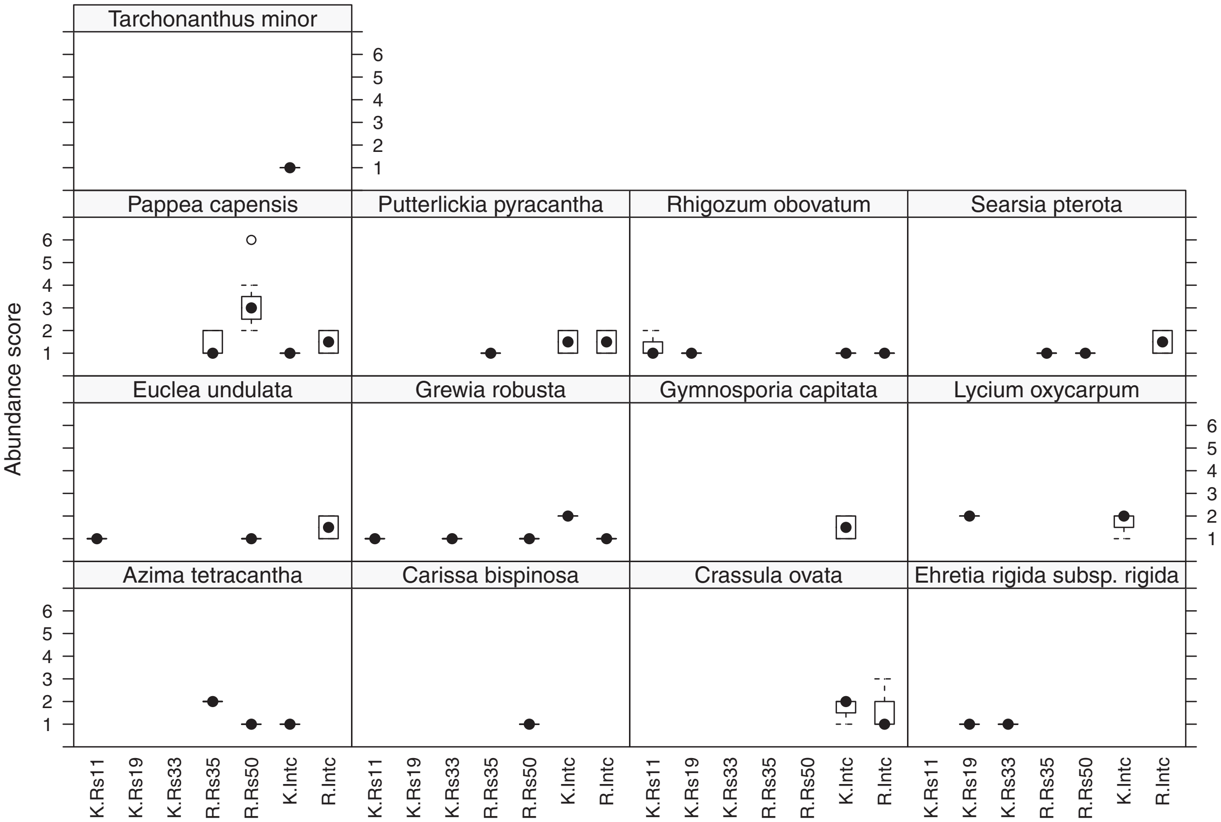

Figure 3. Box plots showing abundance scores of recruits (individuals ≤ 1 m) from canopy species recorded in the different treatments. See Table 1 for explanation of score categories. Prefix "R." denotes stands at Rhinosterhoek, and prefix "K." stands at Krompoort. "Rs" is restored stands and the number appended indicates the number of years under restoration. "Intc" represent intact stands. No recruits were recorded in the degraded stands.

observed a concomitant increase in the abundance of woody canopy recruits, a major functional group in intact Sundays spekboomveld (Vlok et al. 2003) and a general increase in phylogenetic α-diversity and turnover (β-diversity). This trend appeared to be stronger at Rhinosterhoek. The presence of woody canopy recruits suggests that abiotic and biotic conditions on 35-year-old and older restoration treatments are conducive to the spontaneous establishment of these species.

However, our results showed several significant departures from the restoration scenario outlined above. This may be a consequence of our "snapshot" experimental design. First, soil carbon stock of the older restored treatments at Rhinosterhoek (Restored35 and Restored50) were lower than that recorded for intact stands sampled by Mills et al. (2005*a*) probably because (1) more time is required for the establishment of biotic processes that facilitate the incorporation litter into the soil as organic carbon (Wardle et al. 2004), or (2) our limited sample size meant that we did not sample areas representative of the full spectrum of intact sites assessed by Mills et al. (2005*a*). A time lag in soil carbon accumulation is also reported for other woodland restoration projects (Williams et al. 2008). Second, aboveground carbon stock of the 50 year post-restoration was higher than the reference treatments, possibly due to better protection of this treatment (enclosed by a circa 2-m high fence) against domestic and indigenous browsers. Third, the sequestration rate observed at Rhinosterhoek was less than half the rate (4.2 t C $\text{ha}^{-2}\,\text{yr}^{-1}$) recorded in a post-restoration treatment of similar age at Krompoort, possibly as a consequence of the spekboom ecotype ("Bergspekboom") used for restoring most of the treatments at Krompoort. Bergspekboom has a robust, upright growth form and does not develop the ground-level skirt characteristic of almost all other spekboom ecotypes. Despite its perceived higher productivity, we do not advocate using the upright ecotype for restoration initiatives outside its native range. Doing this would compromise the integrity of the projects in terms of achieving overall biodiversity goals, including the maintenance of the genetic structure of spekboom populations. The use of the upright ecotype characterized by an absent basal "skirt" (and thus less of the associated shaded microsite) at Krompoort may explain the low incidence of woody canopy recruits (Sigwela et al. 2009), species richness, and turnover in the 33-year post-restoration treatments (1% of total recruits) compared to the 35 year one at Rhinosterhoek (7%). Light annual browsing pressure from domestic goats may be another reason. These anomalies might not have manifested had we had access to a well-designed experiment with replicated treatments instead of within-treatment subsamples. However, long-term restoration experiments are rare, thereby necessitating the need to exploit

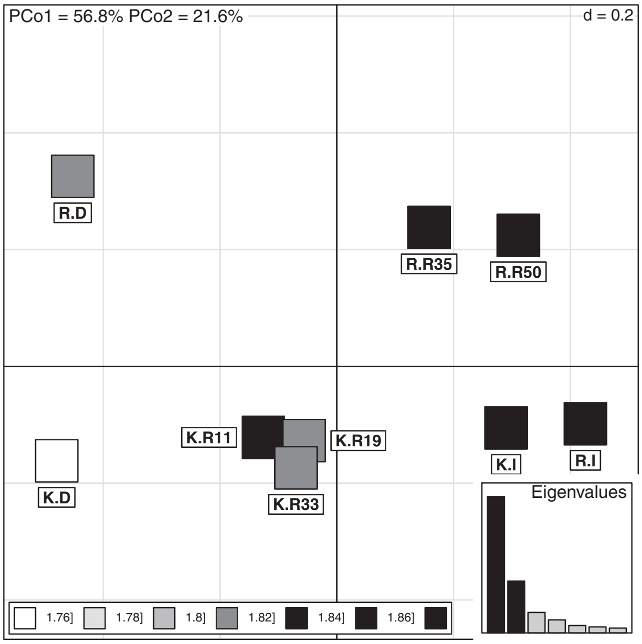

Figure 4. Dimensions one and two of a principal coordinate analysis of rate of turnover *sensu* Jost (2007), as measured by Rao's Q, and taking account of phylogeny. All indices converted to Hill numbers or true diversity (see Methods). Alpha-diversity within each restoration category is shown using shades of grey (see the legend at bottom-left of the figure). Prefix "K." signifies Krompoort site, prefix "R." signifies Rhinosterhoek site, and suffixes "I" and "D" signify intact and degraded stands, respectively. Suffix "R." with a number attached signifies stands under restoration, with the number of years of post-restoration treatment. The darker shaded squares signify a higher α-diversity score, the lighter ones a lower score. The closer the labels are together the lower the turnover between the stands. The primary dimension (x-axis or PCo1) is roughly twice as important (56.8%) as the second dimension (y-axis or PCo2 = 21.6%). Collapsing labels vertically onto the x-axis gives the canonical summary of rate of turnover, and therefore of the floristic similarity between stands.

snapshot ones despite pseudoreplication and design flaws (Michener 1997).

Anomalies aside, planting spekboom truncheons in rows in degraded Sundays spekboomveld appear to shift the ecosystem, after 35–50 years post-restoration, from a degraded state, dominated by remnant and ailing woody canopy trees in a sparse matrix of ephemeral herbs, to one that approximates the intact state both structurally and functionally. Owing to its relatively rapid growth under semi-arid conditions and high litter production (Lechmere-Oertel et al. 2005*a*, 2008), restoration using spekboom produces, within three to five decades, a shaded and carbon-rich microclimate (Mills et al. 2005*a*; Sigwela et al. 2009; Cowling & Mills 2010) that enables the recruitment, via ramets or genets, of woody canopy and other thicket species. In this process, spekboom appears to behave like an ecosystem engineer, defined as an organism that physically creates, maintains or modifies habitats by causing physical state changes in abiotic and biotic materials and thus governs the accessibility of resources to other organisms within the system (Jones et al. 2010). Given their ability to overcome abiotic thresholds, ecosystem engineers are generally regarded as important target species for restoration initiatives (Byers et al. 2006). In this context, spekboom emerges as the ideal candidate for restoring spekboom-dominated Arid Thicket and we think it unnecessary to introduce other plant species as part of the restoration protocol in an effort to return biodiversity. Such introductions may only be necessary in the unusual situations where landscapes lack sufficient area of intact habitat that provides source populations for spontaneous recruitment (Brudvig 2011), or where there is a need to restore populations of locally endemic species.

Implications for Practice

- Degaded landscapes may be restored through actively planting only one or a few critical species. Such species take on the function of ecosystem engineers to restore the landscape by altering the abiotic environment enough for other species, characteristic of intact reference sites, to re-establish spontaneously.
- This type of restoration methodology takes time (almost half a century in our case); this implies high opportunity costs which can be offset through the sale of carbon credits.
- It is important to source propagules of ecosystem engineers for restoration from local populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (a) Contrast between 50-year-old restored thicket (left) and degraded thicket (right) at Rhinosterhoek study area. The dominant shrub in the restored thicket is spekboom (*Portulacaria afra*), towering above the 2-m enclosure fence. Remnant trees in the degraded state are *Pappea capensis* (in the background). Photo: ML van der Vyver. (b) Krompoort study site showing different aged restoration stands (bright green patches) and surrounding degraded thicket with remnant thicket clumps and isolated trees in a matrix of bare ground, ephemeral grasses and karroid shrubs. Photo: RM Cowling. (c) A landscape close to Rhinosterhoek study site. In the foreground is a circa 5-year-old spekboom restoration plot with established spekboom truncheons (bright green shrubs in the foreground) and remnant canopy trees (mostly *Pappea capensis*) enclosed within a stock-proof fence. Behind and upslope of the fence a savanna-like degraded landscape is visible devoid of spekboom which abruptly switches over, where a fence used to be, to intact spekboom thicket further upslope. Photo: ML van der Vyver.

Figure S2. Location map of the experimental sites Krompoort (−33.544690; 25.174098) and Rhinosterhoek (−33.478846; 24.917472) shown in yellow. Green shading represents intact spekboom thicket while red shading represent areas where spekboom thicket landscapes are moderately to heavily degraded (Lloyd et al. 2002).

Figure S3. Google Earth image of Krompoort study area showing the Intact (cyan), Degraded (pink), Restored33 (red), Restored19 (yellow), and Restored11 (blue) sampling sites.

Figure S4. (a) A photograph of Rhinosterhoek taken circa 1960. The planted row of spekboom is already visible where it was planted behind the house (red ellipse). (b) A Google Earth image of Rhinosterhoek showing the different stands, sampled. Red shows the 50-year post-restoration, and yellow the 35-year post-restoration stands, respectively. Pink shows the degraded, and cyan the intact stands, respectively.

Figure S5. Partial results from a bootstrap-analysis of pairwise beta-diversity for selected restoration categories in our study. Each histogram shows the results of 2,000 bootstrapping iterations (or estimates of beta-diversity), here of the species-neutral.

Table S1. Alpha-diversity, evenness and rate of turnover (multiplicative β-1) as measured by species-neutral and species-sensitive (phylogenetic-based) versions of species richness (α-diversity only) and Rao's quadratic entropy (Q), following conversion to true diversity sensu Jost 2007. Recruits were treated as pseudo-species.