Regeneration dynamics of *Portulacaria afra* in restored succulent thicket of South Africa

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Introduction: Over-grazing by livestock has resulted in the widespread degradation of South Africa's succulent thicket ecosystems. This is characterised by a significant reduction in the cover of the dominant succulent shrub, *Portulacaria afra*. Because this species is unable to regenerate naturally in degraded habitat, active reintroduction is required to restore ecosystem function. However, reintroduction success is relatively low, and the recruitment barriers for this species are poorly understood.

Methods: By conducting pairwise plot surveys in actively restored and adjacent degraded succulent thicket habitats, the extent of *P. afra* seedling abundance in these contrasting ecosystem conditions is quantified.

Results: Seedling abundance was significantly greater in restored ecosystems ($W = 23$, $p = 0.03225$). Additionally, seedlings found in restored habitats were strongly associated with open habitat, whereas seedlings in degraded ecosystems were more restricted to nurse sites ($X^2 = 122.84$, $df = 2$, $p\text{-value} < 2.2e\text{-}16$). A weak ($R^2 = 0{,}237$), but significant ($p = 0{,}0295$) correlation between *P. afra* cover and seedling abundance was recorded.

Conclusion: Active restoration of succulent thicket habitat through *P. afra* reintroduction appears to overcome recruitment barriers. This may suggest that, despite the poor survival of introduced individuals, natural recruitment could contribute to the regeneration of restored succulent thicket ecosystems.

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12 ## Abstract

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30 ecosystems.

31 ## Introduction

32 The delicate balance of biotic and abiotic interactions that maintain the persistence of arid/semi-
33 arid (dryland) ecosystems is particularly vulnerable to disruption, making these systems prone
34 to transitioning into a degraded state (Verwijmeren et al., 2013; Aronson et al., 1993). Once
35 degraded, drylands often lack the resilience to naturally regenerate and may require active
36 restoration (Shackelford et al., 2021; Aronson et al., 1993). The ecological success of these
37 restoration efforts is frequently evaluated based on the return of vegetation structure, species

38 diversity, and indicators of ecosystem functioning (Wortley et al., 2013). Here, the recruitment
39 dynamics of *Portulacaria afra* Jacq., the target plant species used in succulent thicket
40 restoration, is compared between restoration plots and adjacent degraded habitat. The data
41 presented here contribute to the growing evidence that succulent thicket restoration facilitates
42 the return of ecosystem functioning.

43 *Portulacaria afra* has long been considered a valuable browse plant in the Eastern Cape of
44 South Africa (Oakes, 1973), supporting the wool and mohair industries over the past three
45 centuries (Beinart, 2008). This prolonged livestock production has led to widespread
46 overgrazing of succulent thicket vegetation, often resulting in the near complete loss of *P. afra*
47 cover. This has shifted the ecosystem from a dense evergreen woodland to a savanna-like
48 vegetation dominated by an ephemeral understorey and bare ground (Lechmere-Oertel et al.,
49 2005). This change in vegetation structure represents a transition that the ecosystem is unlikely
50 to recover from unless actively revegetated (Lechmere-Oertel et al., 2005). Succulent thicket
51 restoration, therefore, focuses predominantly on the reintroduction of *P. afra.* The feasibility of
52 this intervention has been tested at scale in a biome-wide experiment, consisting of
53 approximately 330 Thicket-Wide restoration Plots (TWPs) established across the distribution
54 range of succulent thicket between the years 2008 and 2009 (Mills and Robson, 2017), which
55 form the basis for the adhoc experiment presented here.

56 The ecological importance of *P. afra* in intact succulent thicket has been well described. This
57 species is capable of facilitating landscape-scaled processes by modifying soil properties (van
58 Luijk et al., 2013; Lechmere-Oertel et al., 2008; Mills and Fey, 2004) and providing the micro-
59 climate required for recruitment of woody canopy species (Wilman et al., 2014; Sigwela et al.,
60 2009). Many of these properties are reported to return in restored ecosystems, including the
61 accumulation of soil organic carbon (Schagen et al., 2021; Mills and Cowling, 2014; van der
62 Vyver et al., 2013) and the recovery of some recruitment dynamics (van der Vyver et al., 2013).
63 The remainder of thicket restoration success has largely been quantified in terms of living *P.
64 afra* individuals present in restoration plots, measured to evaluate different planting treatments
65 implemented in the TWPs (van der Vyver et al., 2021a; Mills and Robson, 2017). With an
66 average of 28% of individuals surviving in large-scale plantings conducted over a 12-year period
67 (Mills and Robson, 2017), this approach would suggest that succulent thicket restoration has a
68 relatively low success rate. Measuring individual survival, however, may under-represent the
69 return of ecological processes and cannot detect whether an ecosystem is capable of
70 regenerating without further intervention.

71 The current perspective on *P. afra* seedling recruitment is that it is rare and sporadic (Sigwela et
72 al., 2009; Midgley and Cowling, 1993), likely requiring nurse plant microsites (Adie and Yeaton,
73 2013). However, these studies were conducted in predominantly intact thicket ecosystems, and
74 no attempts have been made to evaluate the extent of seedling recruitment in the patchy cover
75 of restored thicket habitat (Figure 1). The data presented here (a snapshot of *P. afra* seedling
76 abundance) suggest that while *P. afra* recruitment may be sporadic, seedlings do establish
77 readily in restoration plots but are absent in adjacent degraded habitat. Thus, indicating a return
78 of natural regeneration dynamics.

Methods

Study sites

81 Of the 330 TWPs, ten were selected for seedling surveys. These ten plots are representative of
82 the ecological range of succulent thicket, including sites located near the northern, southern,

83 and eastern limits of the vegetation's distribution (Figure 1). Some TWPs were mistakenly
84 established near valley bottoms in an adjacent, frost-prone habitat not suitable for *P. afra* (Duker
85 et al., 2015, 2020), while others were subject to livestock browsing after being established (van
86 der Vyver et al., 2021b). Therefore, not all TWPs were suitable for inclusion in this study, and
87 any plots with reported survival below 20% were excluded from selection. The ten TWPs
88 included in this study all occurred within a matrix of degraded succulent thicket and had some
89 degree of intact fencing, however, evidence of herbivory was present in many of the plots (signs
90 of browsing and dung). Approval for field surveys was acquired verbally from all landowners (S.
91 Nelson, H. Steyn, L. Wright, A. Botha, H. Bekker, T. Murray, M. Wienard, D. van der Decke, and
92 C. Comely) prior to conducting the surveys.

93 As the TWPs were not established with the intention of testing the contribution of revegetation to
94 seedling recruitment, the adjacent degraded habitat did not include any fenced-off control. This
95 study, therefore, represents an ad hoc experiment, where the degraded control sites reflect a
96 range of different management practices, including stocking of livestock and/or indigenous
97 game.

Seedling surveys

99   All surveys were conducted in July 2021, following a severe multi-year regional drought (Archer
100 et al., 2022), and 12–13 years after the initial *P. afra* reintroduction. The full extent of each TWP
101 (50 x 50 m) was surveyed and at each sampling plot, *P. afra* cover was visually estimated
102 (Table 1). All seedlings encountered were documented, and their relative position in reference
103 to a possible nurse shrub was noted. Seedlings were defined as individuals that were either
104 obvious seedlings that had recently germinated or exhibited a typical "mat" above-ground
105 morphology and red pigmentation (Figure 2). Seedlings were either located directly below a
106 nurse shrub, on the edge of a nurse shrub canopy, or in an open habitat defined as bare ground
107 and thus, not associated with any nurse plants. For each TWP a 50 x 50 m quadrat was marked
108 out in the adjacent degraded thicket habitat (Figure 1). The full extent of these quadrats were
109 surveyed, and all seedlings were documented in the same manner as before. The number of
110 seedlings detected in degraded thicket plots was insufficient to draw conclusions on the
111 tendency for *P. afra* recruitment to be associated with nurse plants outside of the fenced-off
112 TWPs (Figure 3). Therefore, two additional 50 x 50 m quadrats were surveyed in a moderately
113 degraded succulent thicket habitat (with an estimated 30% *P. afra* canopy cover) identified by a
114 landowner. These two quadrats covered the majority of the accessible area described by the
115 landowner and were located in a portion of the property managed for indigenous game hunting.

116 The ten TWPs surveyed in this study were distributed across a range of succulent thicket
117 community types. The understorey plant community was, therefore, highly variable across
118 locations, and no trend for specific nurse species could be evaluated. Rather, each site had its
119 own suite of nurse shrubs, predominantly taking the form of dwarf shrubs originating from
120 neighbouring habitats.

Data analysis

122 Differences in seedling abundance between restored and degraded succulent thicket was
123 determined via Wilcoxon rank sum tests for non-parametric data (Hollander and Wolfe, 1973).
124 Differences in the likelihood of seedlings being located in nurse sites between restored and
125 degraded thicket were determined from Pearson's Chi-squared tests of independence (Hope,
126 1968). The correlation between seedling abundance and *P. afra* cover was evaluated using a

127 general linear model (Wilkinson and Rogers, 1973). It was evident that site-specific
128 management of the degraded habitat had no effect on seedling recruitment, as seedlings were
129 rare in all degraded sites, no additional analyses were conducted to account for management
130 practices. All data were analysed using base R, version 4.2.0 (RStudio Team, 2022).

Results and discussion

131

132 Overcoming barriers to unaided recruitment of target species is a major challenge in ecosystem
133 restoration (Fick et al., 2016; Acácio et al., 2007; Standish et al., 2007). Lack of plant density
134 (seed sources) coupled with predation, increased seed loss by wind and rain, and the loss of
135 suitable germination sites promote recruitment failure from a reduced seed pool (Volis, 2019).
136 The decline in ecosystem condition is well described in degraded succulent thicket habitat. The
137 loss of the *P. afra* canopy exposes soils to the elements; leading to the loss of organic content
138 (Lechmere-Oertel et al., 2008; Mills and Fey, 2004), reduced water holding capacity (Mills and
139 de Wet, 2019; van Luijk et al., 2013), increased light exposure, and extreme fluctuations in soil
140 temperature (Lechmere-Oertel et al., 2008). This could potentially eliminate suitable germination
141 sites for *P. afra*, disrupting natural regeneration.

142 Despite the harsh abiotic conditions present in degraded thicket habitat, *P. afra* seed does
143 exhibit the ability to germinate (Figure 3). Seedlings of various growth stages (Figure 2) were
144 detected in degraded and restored habitat, suggesting that seedlings can establish once
145 germinated. The lack of recruitment in degraded thicket may, therefore, be best described as a
146 consequence of seed limitation due to a lack of plant cover, rather than a lack of suitable
147 germination sites. This is supported by a weak (R^2 = 0,237), but significant (p = 0,0295)
148 correlation between *P. afra* cover and seedling abundance, and the fact that seedlings were
149 detected in degraded succulent thicket habitat with limited cover (Table 1). The active
150 reintroduction of *P. afra* appears to overcome this seed limitation. More seedlings (W = 23, p
151 = 0.03225, Figure 3) were found in restoration plots (total seedlings in all TWPs = 477, mean =
152 47.90 seedlings/plot, SD = 97.20, DF = 9) than in adjacent degraded habitat (total seedlings in
153 paired degraded plots = 7, mean = 0.7 seedlings/plot, SD = 1.34, DF = 9). Further work is,
154 however, required to better describe the interplay between canopy cover, herbivory, and
155 recruitment, as sites with high canopy cover (e.g., 90 %) did not appear to support seedlings
156 (Table 1).

157 Seedling microhabitat frequency differed between degraded and restored plots (X-squared =
158 122.84, df = 2, p-value < 2.2e-16). Seedlings found in fenced-off restoration plots (N = 477)
159 tended to occur in open, exposed sites (69.2%) more frequently than elsewhere (9% found on
160 the edge of shrub canopies and 21.8% below a nurse shrub). Seedlings established in
161 degraded thicket (N = 186, including the additional two targeted quadrats) were found 49.5% of
162 the time beneath a canopy of nurse shrubs, 28.5% of the time on the edge of a canopy of nurse
163 shrubs, and 22% of the time in the open.

164 Recruitment of plant propagules is strongly associated with intact succulent thicket habitat that
165 supports dense stands of *P. afra* (Sigwela et al., 2009). The cool, moist microclimate created by
166 dense vegetation cover in this dryland ecosystem is postulated to mimic the subtropical
167 conditions in which much of the thicket canopy tree species originated, facilitating germination
168 and recruitment (Wilman et al., 2014). The loss of canopy cover, therefore, halts broad
169 community assembly processes in degraded succulent thicket, evident in the general lack of
170 seedlings reported in degraded thicket (Sigwela et al., 2009). Restoring this canopy by planting
171 *P. afra* appears to reverse this loss of ecological functioning by regenerating soil organic carbon
172 (Schagen et al., 2021; van der Vyver et al., 2013; Mills and Cowling, 2006) and providing a cool,

173 shaded microclimate. This has facilitated the return of natural recruitment of woody canopy
174 species within 35 years of *P. afra* reintroduction (van der Vyver et al., 2013) and the
175 regeneration of soil bacterial community compositions within 12 years of *P. afra* reintroduction
176 (Schagen et al., 2021). In the ad hoc experiment presented here, significant returns of *P. afra*
177 recruitment were detected 12–13 years after restoration intervention. Thus, this further
178 contributes to the growing body of evidence that the active reintroduction of *P. afra* is a suitable
179 intervention for the restoration of degraded succulent thicket ecosystems. However, while the
180 presence of *P. afra* is required to produce seed for recruitment, unlike other thicket species,
181 canopy cover and nurse shrubs do not appear to facilitate the germination of this ecologically
182 significant species.

183 Open sites are hotter (Lechmere-Oertel et al., 2008) and drier (Adie and Yeaton, 2013) than
184 below plant canopies, yet *P. afra* seedlings appear capable of germinating in these sites in
185 degraded and restored habitats, even during a prolonged and severe drought (Archer et al.,
186 2022). This is likely enabled by multiple adaptations. Firstly, *P. afra* can shift between C3 and
187 CAM photosynthetic pathways, ensuring productivity during hot, dry conditions (Guralnick and
188 Gladsky, 2017; Ting and Hanscom, 1977). Furthermore, seedlings exhibit a red pigmentation
189 (Figure 2), likely due to high levels of anthocyanins, which may contribute to tolerating aridity,
190 UV radiation, and extreme temperature fluctuations (Chalker-Scott, 1999).

191 As the open sites are comparable between restored and degraded plots, both are composed of
192 bare soil, lack organic matter, and are exposed to direct sunlight, the different spatial patterns of
193 seedling recruitment described for restored and degraded habitats are unlikely a consequence
194 of abiotic conditions. Rather, the association of *P. afra* seedlings with nurse shrubs, argued to
195 be part of a cyclic succession process by Addie and Yeaton (2013), is more likely due to
196 herbivory protection in open and actively browsed habitats. The sampling sites in this study all
197 supported livestock and/or indigenous game (reduced in TWPs due to fencing), whereas the
198 study site in Addie and Yeaton (2013) supported livestock in a relatively intact succulent thicket.
199 Thus, the tendency for *P. afra* seedlings to be associated with nurse shrubs is unlikely to be
200 indicative of landscape-wide community assembly patterns, as suggested by Addie and Yeaton
201 (2013), but rather, a consequence of herbivore density.

202 Herbivory can act as a barrier to the recruitment of palatable target species in restoration
203 initiatives (MacDougall and Wilson, 2007; Opperman and Merenlender, 2000). Herbivory was
204 found to be one of the key determinants of reintroduced *P. afra* survival in the TWPs that
205 provided the basis for this study (van der Vyver et al., 2021b). In cases where the fenced
206 enclosures were removed (either intentionally by landowners or accidentally by large animals),
207 *P. afra* reintroduction success was markedly reduced, with no plants surviving in some
208 instances (van der Vyver et al., 2021b). It should, however, be noted that the restoration plot
209 with the second highest seedling density (84 seedlings recorded) exhibited clear signs of
210 browsing and the fence had been pushed down by cattle in recent years (i.e. the reintroduced *P.*
211 *afra* were well established before being exposed to browsing by livestock). This could imply that
212 once established, restored succulent thickets can withstand some browsing without
213 compromising local regeneration patterns, but the carrying capacity of restored succulent thicket
214 must be closely monitored.

Conclusion

216 One of the major challenges facing the restoration of dry ecosystems is overcoming barriers to
217 seedling establishment. The restoration of succulent thicket ecosystems relies predominantly on
218 the reintroduction of the target plant species *P. afra*, which exhibits rare and sporadic

219 recruitment from seed. This intervention appears to ameliorate seed set limitations, promoting
220 the recruitment of this species in restored habitats. No evidence of nurse plants facilitating
221 seedling establishment was detected in fenced restoration plots, however, seedlings were
222 commonly associated with nurse plants in degraded sites exposed to greater levels of herbivory.
223 Nurse shrubs do not, therefore, appear to be tied to *P. afra* recruitment as previously
224 suggested. To facilitate the return of recruitment dynamics in restored succulent thicket,
225 herbivore pressure should be reduced and/or restoration should target ecosystems with low
226 herbivore densities.

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Figure 1

An example of a Thicket Wide Plot (TWP) and the distribution of the ten TWPs surveyed for *Portulacaria afra* seedlings.

The paired sampling quadrats are indicated with red dashed lines. Note the three distinct vegetation conditions, restored *P. afra* cover in the TWP in the foreground, the open savanna-like habitat (degraded thicket) surrounding it and the densely vegetated hills in the background (intact thicket). The spatial distribution of the ten TWP surveyed is provided in the top right inset (Maps data: Google, SIO, U.S. Navy, NGA, GEBCO), which is contextualised as a red polygon in relation to South Africa to the left of the inset.

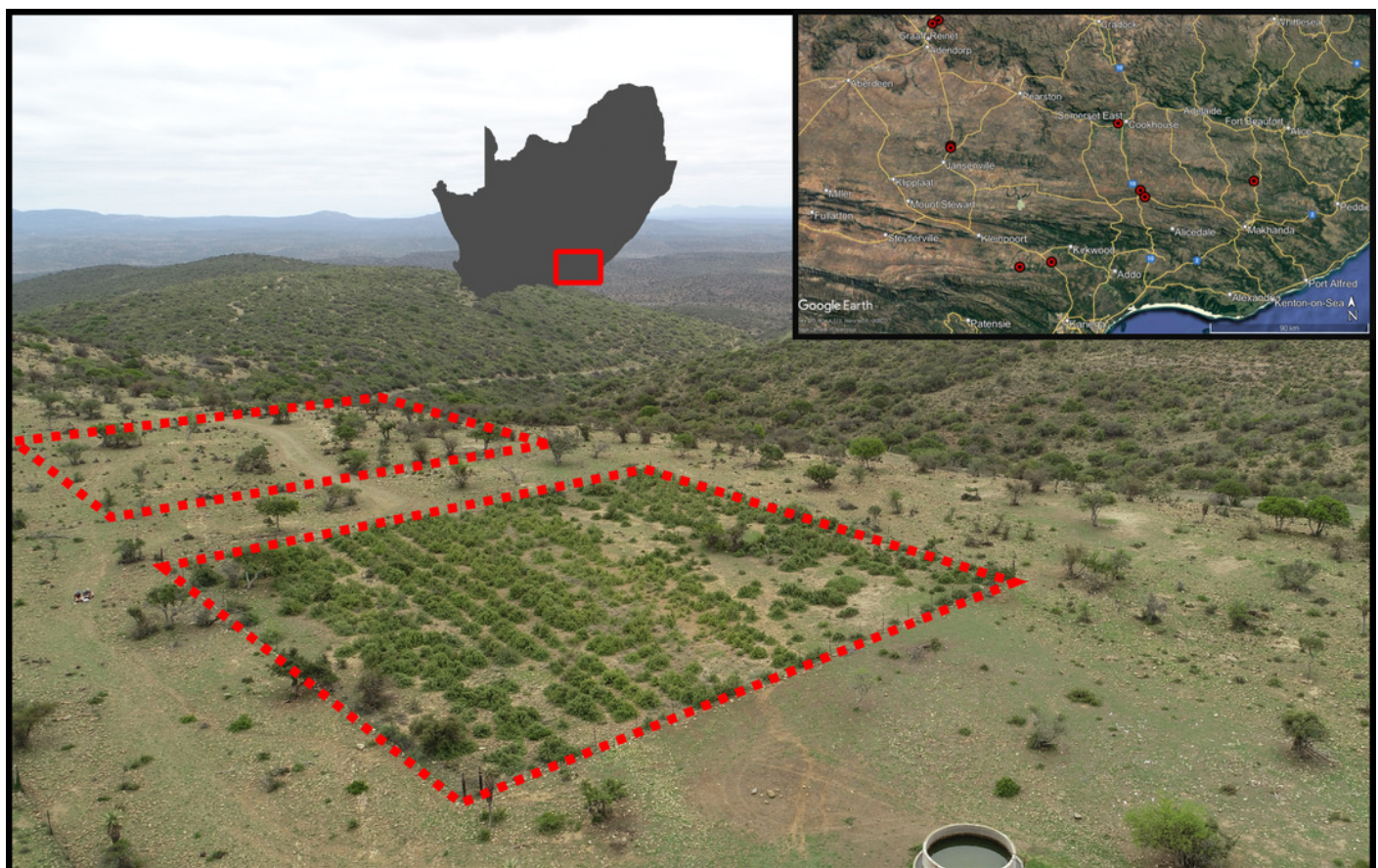



Figure 2

Portulacaria afra seedling morphology.

A) A reecntly germinated *P. afra* seedling (likely from within the past year), note the distinct red pigmentation. B) The primary stem tends to exhibit lateral growth to create a hooked morphology as the seedling establishes. C, D) This lateral growth is continued by side branches to form a mat before initiating vertical growth. Note that all the morphologies depicted here were considered seedlings in the surveys as they had not matured to a point that they exhibit vertical growth or the loss of the red leaf pigmentation typical of juvinile *P. afra*. Any individuals with green leaves or vertical branches were not considered seedlings.

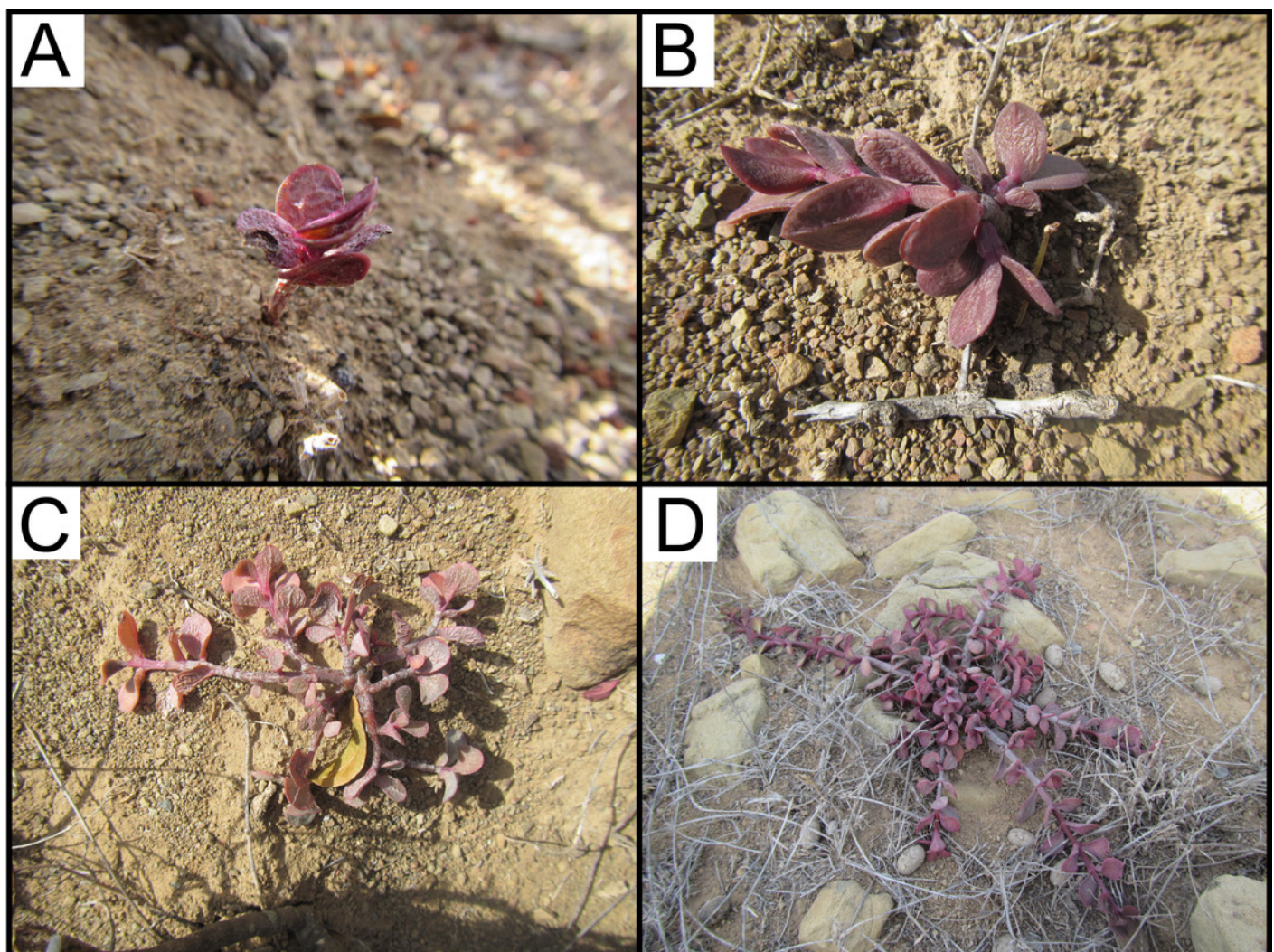
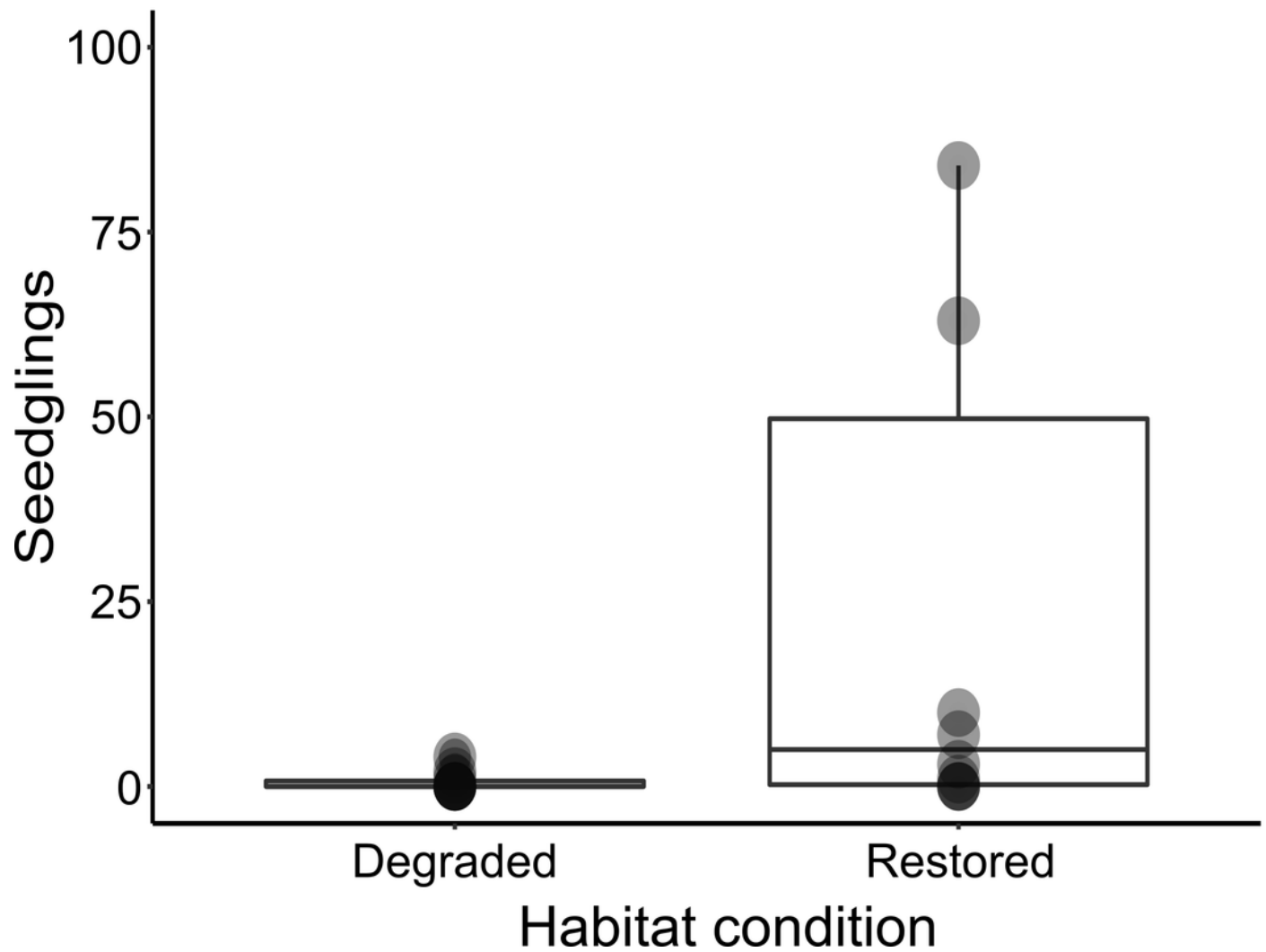



Figure 3

Box-plot comparing seedling abundance between restored and degraded succulent thicket habitat.

Portulacaria afra canopy cover and seedling abundacne recorded in each 50 x 50 m quadrat.

All degraded sites were exposed to some degree of herbivory (either livestock and/or native browsers) whereas the restored sites were fenced off to limit browsing. Some evidence of browsing was however evident in many of the restoration plots (i.e., animal paths and dung), but to a far lesser degree than in the degraded sites.

Plot ID	Degraded		Restored	
	P. afra cover	Seedlings (count)	*P. afra* cover	Seedlings (count)
p0008	10	2	7	1
p0014	0	0	60	311
p0032	5	4	55	84
p0035	0	0	90	0
p0058	0	0	45	3
p0089	0	0	35	7
s0015	0	0	40	63
s0045	0	0	10	0
s0081	0	1	10	10
s0093	0	0	10	0