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TECHNICAL ARTICLE

Field surveys and revegetation experiments show that simulation of topographical habitat features could improve the chances of successful restoration for the threatened succulent *Juttadinteria albata*

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Species with highly restricted ranges are disproportionately at risk of extinction, particularly where habitat loss occurs as a result of mining. Postmining restoration of rare species populations is considered as an appropriate response to counter such threats, but requires a careful, evidence-based, and information-driven approach. The economically important diamond mining at Sendelingsdrif in the southern Namib Desert occurs in the highly diverse Succulent Karoo Biome and threatens a significant part of the population of the narrow endemic succulent plant species *Juttadinteria albata*. To decrease the inherent risks of restoring such a rare species, we studied the habitat features of premining *J. albata* populations and experimentally tested whether some features could assist future reintroductions in postmining substrates. Plots where *J. albata* occurred were mostly south- to west-facing and had among others higher rock cover and steeper slopes than plots where *J. albata* plants were absent. A revegetation experiment, with *J. albata* cuttings that were established on postmining substrate mounds, revealed that plants on steeper slopes, facing south to west, grew faster than plants on other slopes and aspects. Slope and aspect are therefore important habitat properties to recreate when restoring *J. albata* populations. These, and other preferred habitat properties such as higher levels of organic C, should now be tested in larger-scale field trials. Validation of habitat requirements of *J. albata* through the revegetation experiment has decreased the risks at least partially and provides additional empirical evidence of the importance of establishing reference conditions to enhance ecological restoration.

Key words: diamond mining, endemic species, habitat requirements, *Juttadinteria albata*, revegetation experiment, Succulent Karoo Biome

Implications for Practice

- Field surveys of habitat preferences and subsequent experimental results suggest that *Juttadinteria albata* should be transplanted (or seeded) onto south-southwest or west-facing steep (>20°) slopes during ecological restoration.
- Other features that proved to explain variation in species occurrence in nature, such as rock cover and organic carbon levels, could theoretically further improve chances of successful establishment. This should be tested at appropriate scales to better understand the mechanisms involved.
- Our study has reinforced the general principle of establishing reference conditions in advance, and testing the application of these in a systematic experiment to facilitate effective ecological restoration.

Introduction

Several studies and reviews have shown that species with highly restricted ranges are disproportionately at risk of extinction (Mace et al. 2008; Pimm et al. 2014), particularly if there are other threats such as habitat loss (Schemske et al. 1994; Brooks et al. 2002; Mace et al. 2008; Brummitt et al. 2015). Restoration of rare species populations is considered to be an appropriate response to counter such threats, but requires a careful, evidence-based, and information-driven approach (Brzosko et al. 2018). The approximately 300 km^2 range of the narrow vulnerable endemic leaf succulent species *Juttadinteria albata* (L. Bolus) L. Bolus (Mesembryanthemaceae) is centered on the

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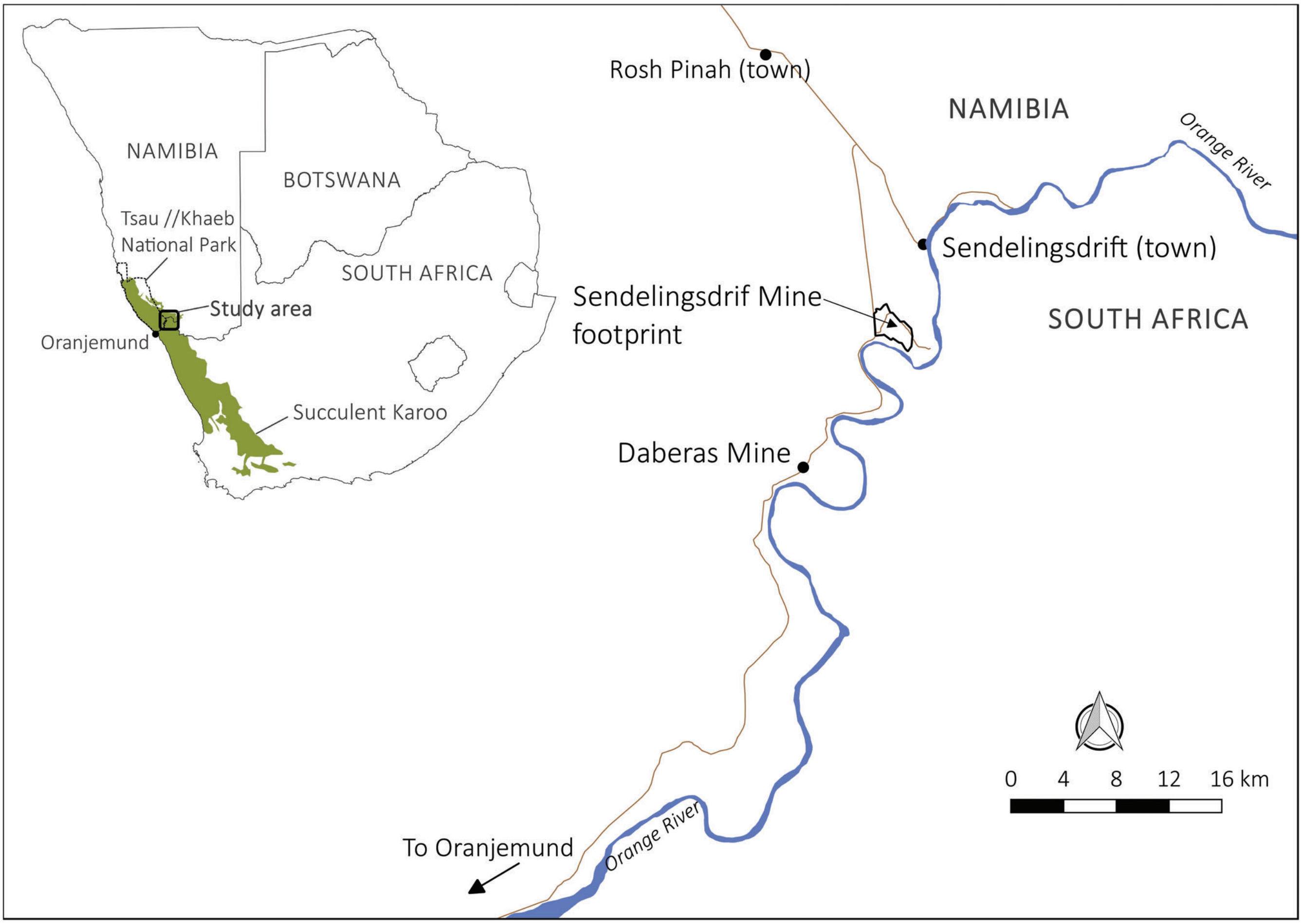

Figure 1. The study area falls in the Succulent Karoo Biome and the Namibian Tsau //Khaeb National Park (inset). The Sendelingsdrif Mine is close to the center of distribution of *Juttadinteria albata*, which also includes, inter alia, Daberas Mine, another Namdeb project. The species' range is not shown here, because the National Botanical Research Institute (NBRI) of Namibia strongly advise against the publication of exact locations of rare and threatened species, as this may increase the risk of unscrupulous collecting (S. Loots, NBRI, Windhoek, personal communication).

Sendelingsdrif Diamond Mine on the Namibian bank of the lower Orange River (Loots 2018). The mine is located within the Tsau //Khaeb National Park and the Succulent Karoo Biome (SKB), a local center of endemism and biodiversity hotspot (Maggs et al. 1998; Cowling 1999; Myers et al. 2000; Loots 2005; Mucina et al. 2006).

Including other mines in the area, the Sendelingsdrif Mine represents a significant additional threat of habitat loss to the species. Consequently, the mining company has undertaken to reintroduce the species after mining as part of a more comprehensive restoration plan (Fortuin 2011). Given the risks of failure associated with restoration in general and with arid land restoration specifically (Aronson et al. 1993), it is important to approach such an initiative with caution. As is the case with reintroduction of plant species anywhere (Dalrymple et al. 2012; Brzosko et al. 2018), particularly for species with highly restricted ranges, the optimization of habitat conditions after mining is likely to be key to success. Previous unpublished studies defined both the geographic range of *J. albata* (Burke 2004*a*) and general landscape categories in the study area (Fortuin 2011), but the species' specific habitat preferences and relationships with key environmental variables were unknown.

Consequently, we approached the restoration of *J. albata* populations after mining as a two-pronged strategy. First, we studied the species in its native habitat to define and quantify the most important or critical habitat features and ecological processes that could potentially be utilized as "natural tools" (cf. Bradshaw 1997) in the design of a restoration strategy. Second, we tested selected factors in a greenhouse experiment and in a slightly larger revegetation trial to refine the strategy.

Anecdotal observations of vegetation patterns, as well as studies of vegetation patterns in the larger SKB (Desmet & Cowling 1999; Burke 2004*b*; Riginos et al. 2005; Carrick & Kruger 2007), suggested a strong filtering effect of physical and, potentially, of chemical soil properties for plants. We therefore aimed to determine relationships of *J. albata* with selected habitat features, hypothesizing that *J. albata* density will be associated with properties such as infiltration rate, rockiness, slope angle, aspect, soil texture, and chemistry. Based on these results, we then tested whether some of the habitat features could be used to assist future reintroduction of the species in the postmining substrates. We drafted recommendations for the next steps, which should include even larger-scaled field trials and a subsequent pilot restoration before a restoration plan is fully implemented.

Methods

Study Area

Sendelingsdrif Mine (28° 9′26.00″S, 16°51′42.74″E) (Fig. 1) is a project of the Namdeb Diamond Corporation (Pty) Ltd., Windhoek, Namibia. Rainfall in this region, which occurs primarily in winter (June–August), is between 11 and 88 mm pa for about 90% of the time with a long-term average of less than 100 mm pa (Williamson 1997; Mendelsohn et al. 2002). Fog, especially advective stratocumulus clouds forming over the Atlantic Ocean and occasionally radiative fog in the river valley itself, occurs occasionally (Mendelsohn et al. 2002). Summer (December–February) temperatures may reach 40°C and the average winter minimum is 12°C. Prevailing winds, for most of the year, are south and southwesterly, but hot easterly winds also occur and are most common in winter (Williamson 1997; Mendelsohn et al. 2002).

The main diamond resource occurs in gravels, deposited in a matrix of loamy sand of fluvial origin as terraces in paleo-courses of the Orange River, of which the early mid-Miocene age "Proto-Orange" terraces are the largest and economically most significant (Jacob et al. 1999).

Research Design

The study was divided into two components: (1) a field survey to search for *J. albata* and determine its preferred habitat properties and (2) a revegetation experiment to determine the optimum combination of slope and aspect for plant growth and survival in landscaped mine tailings. This experiment was based on the findings from our field survey and our earlier observations of differential plant growth related to topography,

Field Survey: Habitat Physical and Chemical Characteristics

A sparse, aggregated distribution (as previously described for *J. albata*; Loots 2005) presents a challenge for estimating any aspect of a plant's population characteristics or habitat preferences. To increase our chances of finding the plants, as well as determine the difference between the habitat properties it prefers and the average properties of the environment, we custom-designed a method that was effectively a random survey coupled with a directed search for the species.

To enable an unbiased survey, seven previously defined landscape units (Fortuin 2011) that contained *J. albata* individuals were used as basis for placing 71 random survey points using ArcGIS mapping software (Environmental Systems Research Institute 2011). At each random point we placed a 4 m × 4 m quadrat in which we counted and measured any *J. albata* individuals present. We then searched around each random point in a circular area with a radius of 150 m until we found the nearest *J. albata* plant. A 50 m × 50 m further search area was defined such that this nearest *J. albata* plant was in the middle of the length of its nearest edge. Within this further search area we looked for a plant cluster with the highest density of *J. albata*. At the apparent mid-point of this local-highest density cluster we then placed another 4 m × 4 m quadrat. We refer to the pair of quadrats as the random and the *Juttadinteria* quadrats respectively. Using this paired-quadrat approach, we aimed to determine how much the environment at the highest local density (as measured in the 4 m × 4 m "*Juttadinteria* quadrat") differed from the average habitat condition (measured in the "random quadrat").

In each quadrat we measured the percentage rock cover, slope, aspect, and infiltration rate and collected soil samples. Percentage rock cover was determined by placing a 1 m ruler successively at the center and four corners of each quadrat and measuring the length of the ruler intercept of each stone (Esler & Cowling 1992). Cover of stones less than 2 cm were visually estimated and added to the total percentage cover. Slope angle was measured using a clinometer and aspect was measured in azimuth degrees using a compass which was subsequently collapsed into eight cardinal directions and one called "level" (slope angle = 0°). Infiltration rate was measured using a mini disk infiltrometer. To sample soil, we removed the surface litter before taking a 10 cm × 10 cm × 10 cm sample from each corner and at the center of the quadrat. Each sample from each corner and at the center of the quadrat was sieved through a 2 mm fraction mesh in the field (Midgley & Musil 1989) and pooled per quadrat, yielding a total sample of approximately 1 kg for each quadrat. To contain costs, soil samples of 24 quadrat pairs were chosen randomly for chemical analyses. Samples were placed in paper bags for transport to the analytical laboratory. All methods used for chemical analyses followed Pansu and Gautheyrou (2006). Prior to analyses in the laboratory soil samples were again sieved through a 2 mm fraction mesh sieve and air dried. Total N was measured using the Kjeldahl method and extractable P was determined using a UV–Vis spectrophotometer (UV mini–1240) method. Organic C was measured using the Colorimetric Walkley–Black method and soil texture was determined using a pipette method and reported as percent clay, percent sand, and percent silt. Nutrients such as Ca, Fe, and Mg were measured using ammonium acetate (1 M) extractions. In each 4 m × 4 m *Juttadinteria* quadrat, we counted each rooted *J. albata* plant. The count data was used to calculate the density of *J. albata* in each 4 m × 4 m *Juttadinteria* quadrat as density = count/area of 4 m × 4 m *Juttadinteria* quadrat (Barbour et al. 1999). We did not find *J. albata* in all 4 m × 4 m random quadrats.

Revegetation Experiment

In the revegetation experiment, *J. albata* was grown on 12 experimental mounds that comprised a 1:1:1 ratio of fine materials (postmining "tailings" comprised of soil particles ≤2 mm diameter), coarse materials (diameter 2 ≤ 25 mm), and oversize

Table 1. Statistical tests used.

Contrast/test	*Variables*	*Statistical test*
Comparing paired *Juttadinteria* and random quadrats	Mean rock cover, infiltration rate, slope angle, and concentrations of total N, organic C, Ca, Fe, Mg, and extractable P in soil	Paired *t* test
Association between soil texture and *Juttadinteria* quadrats	Proportion of sand, loam, clay in each quadrat	χ^2 test
Association of *J. albata* with aspect of slope	Presence or absence of *J. albata* in quadrats located on slopes facing in one of eight cardinal directions	Median test
The effect of aspect and steepness of slope on canopy growth of cuttings of *J. albata*	Canopy volume of cuttings	Repeated measures analysis of variance test. Measurements taken in March (within weeks of transplantation), May, September, and November 2013 were entered as the within-subject in the model. Aspect at eight different cardinal wind directions plus one called "level" (slope angle = 0°) and steepness of mound slopes (gentle vs. steep) were entered as factors.
Differences between factor levels at the end of the experiment	Canopy volume of *J. albata* cuttings.	Analysis of covariance with post hoc Tukey's tests. November 2013 canopy volume as dependent variable, slope and aspect as factors, and March 2013 canopy volume as covariate

materials (diameter $25 \leq 50$ mm). The tailings were obtained from an existing exploration plant at Sendelingsdrif Mine. The 12 experimental mounds had a basal diameter of 5 m and were erected in two rows 30 m apart and spaced about 15 m apart within each row.

The experimental layout followed a factorial experimental design. The two factors were slope, applied at two levels (steep: 27° and gentle: 20°), and aspect at eight different cardinal wind directions and one called "level" (slope angle = 0°). Six experimental mounds had gentle slopes (0.79 m high) and the other six had steep slopes (1.23 m high). The position of each experimental mound was determined using random numbers generated in Microsoft Excel. Cuttings of *J. albata* plants rescued from areas where strip mining for diamonds is planned were transplanted on the experimental mounds after an opportunistic rain event. Prior to transplanting, the cuttings were air dried in a shade-net greenhouse for 24 hours to reduce the risk of infections. Each of the nine aspects received three cuttings and was irrigated with 5 L of water on three alternating days a week for 3 weeks. Irrigation intensity was subsequently decreased to 4 L once a week for 4 weeks and finally to 4 L twice a month for 2 months. We measured, to the nearest cm, four times in 9 months (during March 2013, May 2013, September 2013, and November 2013 respectively) the height (H) and diameter of the canopy of each cutting along two axes of a theoretical oval shape (L and W) and used these to calculate the ovoid canopy volume as $4/3\pi(L/2)(W/2)(H/2)$) (Esler & Cowling 1992).

Data Analyses

STATISTICA (version 7.1) software was used for all statistical analysis of data (StatSoft Inc. 2005). All data were tested for normality using the Shapiro–Wilk test. Homogeneity of variances was tested using Levene's test on the data on which analysis of covariance and repeated measures analysis of variance were subsequently carried out. The canopy volumes at the start of the experiment (March 2013) was entered as a covariate in the model. Data on infiltration rate, slope angle, concentrations of Fe, total N, organic C, and Mg in the soil, canopy volumes of cuttings in different aspects, and slope types on experimental mounds were not normally distributed and were therefore logarithmically transformed. These transformed data were then analyzed using appropriate parametric statistical tests (Table 1). Means obtained from transformed data are reported in their untransformed form.

Results

Habitat Physical and Chemical Characteristics

None of the 4 m × 4 m quadrats placed at the random points had any *J. albata* plants growing in them, while only 41 random points had *J. albata* plants growing in the surrounding circular search area with a 150 m radius. *Juttadinteria* quadrats had significantly higher mean rock cover ($t = 6.40$, $df = 40$, $p < 0.001$) and slope angle ($t = 6.30$, $df = 40$, $p < 0.001$) but a significantly lower infiltration rate ($t = -3.19$, $df = 40$, $p < 0.01$) than those calculated or measured in their paired random quadrats (Table 2). In the field, *J. albata* was strongly associated with specific aspect positions. Compared to the randomly located quadrats, *Juttadinteria* quadrats were frequently facing in a southern, southwestern, and western direction (Fig. 2). In contrast, the majority of randomly selected quadrats were found on flat terrain (Fig. 2). A median test showed that the frequency

Table 2. (A) Mean (±SE) rock cover, infiltration rate, and slope angle, and the differences between the means for *Juttadinteria* and random quadrats (difference is *Juttadinteria* minus random). The results of paired *t* tests are also provided. Sample size was 41 and *df* were 40 in all cases. (B) The number of random and *Juttadinteria* quadrats in each of three soil texture classes. Sample size was 48 (24 for *Juttadinteria* and random quadrats each).

Variable	Juttadinteria *quadrats*	*Random quadrats*	*Difference*	t (df = *40)*	p *value*
(a) Rock cover, infiltration rate, and slope angle					
Rock cover (%)	69.98 ± 3.41	38.55 ± 3.80	31.43	6.40	<0.001
Infiltration rate (cm/s)	0.01 ± 0.002	0.02 ± 0.01	−0.01	−3.19	<0.01
Slope angle (°)	14.07 ± 1.26	5.90 ± 1.15	8.17	6.30	<0.001
(b) Soil texture ($\chi^2 = 0.14$, $df = 2$, $p = 0.93$)					
Sand	13	18			
Loamy sand	8	5			
Sandy loam	3	1			

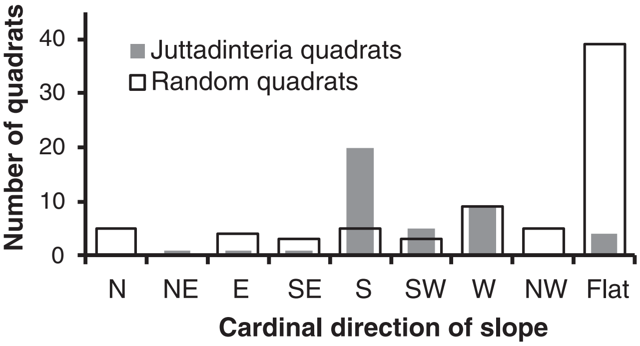

Figure 2. The frequency of occurrence of random quadrats (*Juttadinteria albata* absent) and *Juttadinteria* quadrats (*J. albata* present) on different cardinal directions of slopes (aspects) in the field survey.

distribution of random and *Juttadinteria* quadrats occurring on different aspects differed significantly ($\chi^2 = 332.3$, $df = 8$, $p < 0.001$). The species did not, however, seem to have a preference for a specific soil texture (Table 2; $\chi^2 = 0.14$, $df = 2$, $p = 0.93$). *Juttadinteria* quadrats had significantly higher mean concentrations of organic C ($t = 3.84$, $df = 23$, $p < 0.01$) in the soil than that found in their associated random quadrats, but the concentrations of total N ($t = 0.44$, $df = 23$, $p = 0.67$), Ca ($t = 0.77$, $df = 23$, $p = 0.35$), Mg ($t = 1.56$, $df = 23$, $p = 0.13$), Fe ($t = -0.63$, $df = 23$, $p = 0.54$), and extractable P ($t = 0.58$, $df = 23$, $p = 0.57$) did not differ significantly (Table S1, Supporting Information).

The Revegetation Experiment

The canopies of cuttings increased in size from March to November (Table S2; Fig. 3). The aspect ($f = 2.29$, $df = 8$, $p < 0.05$) where plants were established influenced the canopy growth rate of cuttings and was more important than the steepness of slope ($f = 3.92$, $df = 1$, $p = 0.05$; Table S2; Fig. 3). Aspect and slope did not interact over time ($f = 0.78$, $df = 8$, $p = 0.62$; Table S2). Plant canopy volumes at the start of the experiment (March 2013) were unrelated to the aspect or slope steepness; they were planted on analysis of variance test ($p > 0.05$), confirming that initial differences in canopy volumes were not biased. Aspect was most important in explaining final canopy volume differences ($f = 5.83$, $df = 8$, $p < 0.001$; Table S3; Fig. 4).

At the end of the experiment (November 2013), cuttings of *J. albata* growing on the level tops of mounds and those on the western, southwestern, and southern aspects were significantly larger than cuttings in the northern, northeastern, eastern, or northwestern aspects (Tukey's test, $p < 0.05$; Fig. 4).

Discussion

Our field survey results showed that the habitat preferred by *J. albata* was steeper and rockier, had slower water infiltration, had more organic C, and was more likely to be oriented towards the southern and western aspects than what is found on average in the study area. In addition, it is apparent from our results that the simulation of only two habitat characteristics, namely slope aspect and steepness, could potentially translate to better growth. Hence, the re-creation of these conditions should result in a larger chance of survival and successful restoration.

The influence of aspect on plant distribution and abundance is a well-known phenomenon (e.g. Sternberg & Shoshany 2001; Farzam & Ejtehadi 2016; Pelletier et al. 2017; Wang et al. 2017). In the southern hemisphere tropics, northern and northwestern aspects present harsher habitat conditions because they face the sun for most of the day, while southern and southeastern aspects tend to be gentler (Esler et al. 2006; Pelletier et al. 2017). However, the preference that *J. albata* seems to have for south-facing aspects in our study area is more likely a result of the local wind and rain dynamics (Cowling et al. 1994; Desmet 2007). There have been no studies on the actual mechanism involved, but it is likely that it is the result of either or both the direction from which rain and fog arrive (with the amount of intercepted moisture being influenced by the steepness of slopes), and the deposition of fine, plant-smothering sands on slopes that lie leeward and perpendicular to the predominant wind directions. While not measured for other plant species in our study area, personal observations suggest that directional and slope angle effects are strong general filters for many plant species here. Landscaping of the postmining environment to include aspects and slopes that capture the processes that will improve plant performance thus represent a type of natural restoration "tool" (cf. Bradshaw 1997). Plants on the level tops of the experimental mounds performed at least as well as on the best slopes, but we believe that this is more likely because

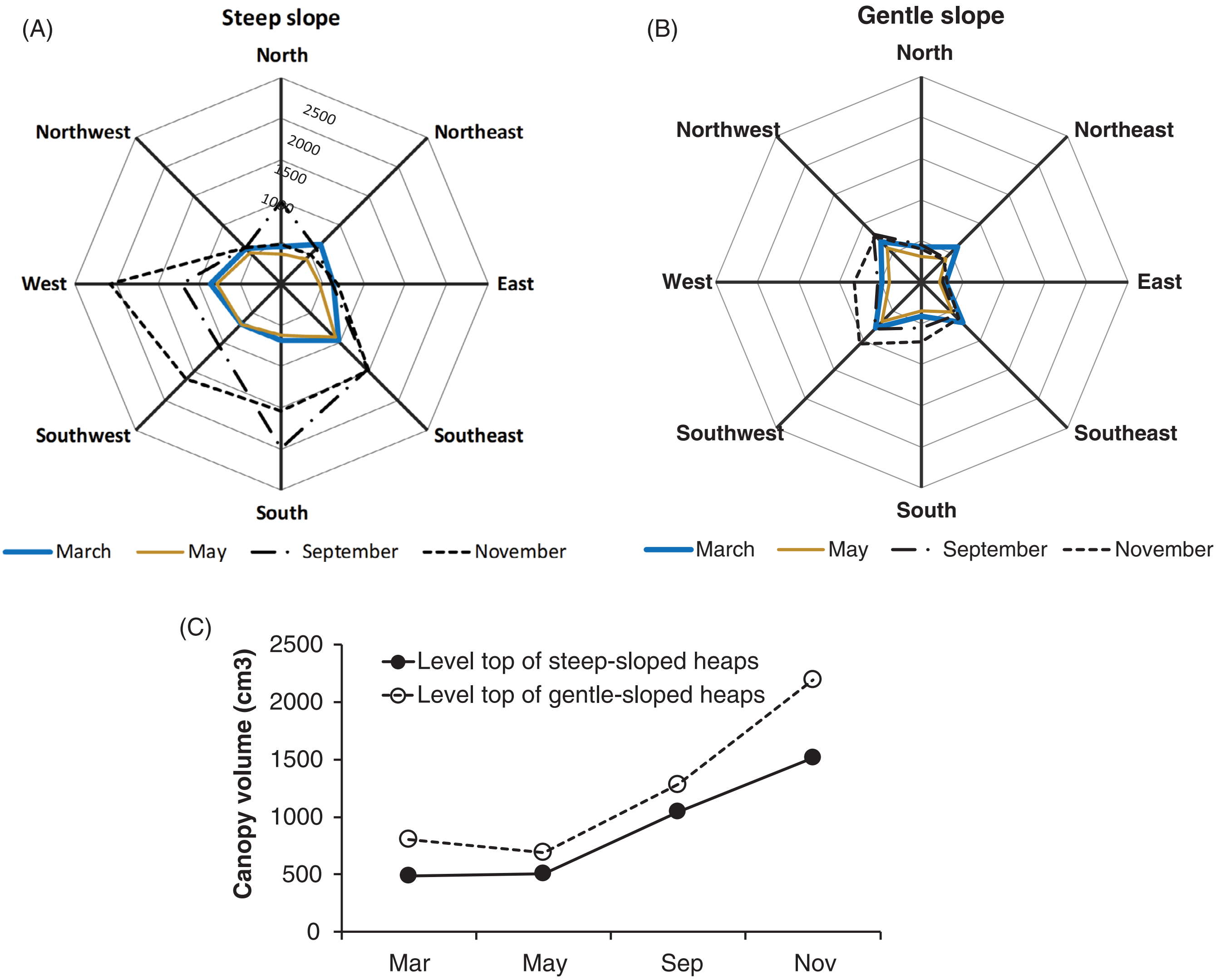

Figure 3. Canopy volumes of cuttings of *Juttadinteria albata* in aspect at eight different cardinal wind directions on steep (A) and gentle (B) slope experimental mounds as well as on the level tops of mounds (C) measured during March, May, September, and November 2013. Axis scaling in (B) is the same as in (A) and the unit is cm^3.

they received relatively more water during irrigation as water ran faster off the sides of the mounds.

The other habitat features that emerged as important explanations of plant density during the field survey are not as simple to translate into restoration approaches. The lower infiltration rate associated with *Juttadinteria* quadrats was unexpected, but was possibly related to the dense loamy soil of ancient fluvial origin in the gravel beds, where many of the plants occurred. We therefore do not think that it will be necessary to recreate poorly infiltrating soils during restoration, but more work is required to understand the mechanisms involved in determining soil moisture dynamics, particularly water infiltration, and how best to use this to increase plant performance. We intend to do this in a larger-scale field trial.

The high affinity for rock cover shown by *J. albata* in our study is perhaps more relevant for restoration. Rocky habitats contribute to ecosystem resilience by creating favorable micro-environments, especially as moisture traps (Poesen & Lavee 1994; Whitford 2002) or by providing direct access to minerals (Lopez et al. 2009). As elsewhere (Maccherini 2006), diversity, especially of endemic species, tends to concentrate on such rocky habitats in the SKB (Cowling et al. 1994; Desmet & Cowling 1999). Such natural physical properties of rocky habitats make them attractive to plants and also make them unique features in the landscape, but are unfortunately extremely difficult to recreate after mining. Still, other properties of a rocky cover, such as its mulching effect (Bainbridge 2007), may be easier to achieve and could positively influence soil moisture dynamics and protect juvenile plants.

Organic C differed between *Juttadinteria* and random quadrats, but the overall levels were low (typical for arid soils; Zhang & Shao 2014) and the difference (0.04%) was marginal

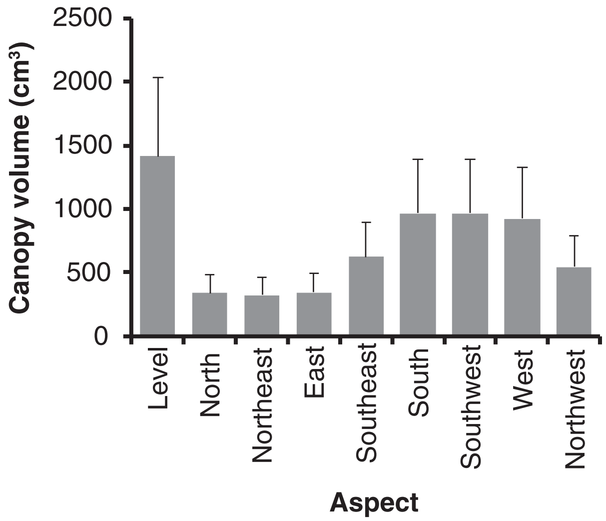

Figure 4. Mean canopy volumes (cm^3) of cuttings of *Juttadinteria albata* in aspect at eight different cardinal wind directions and one called "level" (slope angle = 0°) at the end of experiment (November 2013). Vertical bars denote +SE.

in terms of what a plant would be likely to respond to. The difference could also reflect the fertilizing effect of the plants rather than their response to preexisting soil fertility (Barth & Klemmedson 1978; Schlesinger & Pilmanis 1998). Whether it would be an important feature to manipulate during restoration is therefore not clear, but we intend testing it as a factor in a greenhouse and larger-scale field trial.

Our study focused on a single species at a specific site in the southern Namib, but our findings do have some more general implications. The usefulness of revegetation experiments is well documented (Klokk & Rønning 1987; Rydgren et al. 1998; Cooper & MacDonald 2000; Glenn et al. 2001; Titus & Titus 2008). This study confirms the importance of revegetation experiments and the necessity of a careful, systematic experimental and scaled approach in establishing viable species reintroductions. Although many species can easily be grown in greenhouses, lack of information regarding specific requirements that allow long-term persistence of the species in natural habitats can hinder restoration programs.

Therefore, the case study that we present here offers a model for the restoration of range restricted plant species in the SKB and similar landscapes where potential factors influencing the distribution or likelihood of occurrence of the species are identified prior to mining operations or developmental projects so as to determine suitable habitats and approaches for restoration purposes. Our case study, in which some habitat requirements of *J. albata* were validated through the revegetation experiments, provides a good example of the need to establish reference conditions (Stoddart et al. 2006) in order to promote effective restoration. The restoration of rare or endemic plant species here will require a careful and measured approach to manage risks of failure. By describing its habitat and testing some potential ecological "tools," we have decreased the risks at least partially.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Mean (±SE) concentrations of minerals in the soil in *Juttadinteria* and random quadrats and the difference between the means as well as the results of paired *t*-tests for differences among means.

Table S2. Statistics of a Repeated Measures Analysis of Variance test with the canopy volume of cuttings of *J. albata* measured in March, May, September, and November 2013 (Time) related to aspect and slope angle of the position on the experimental mounds where cuttings were transplanted in February 2013.

Table S3. Statistical results of an Analysis of Covariance with the canopy volumes (logarithmically transformed) of cuttings of *J. albata* at the end of the experiment (November 2013) related to aspect and slope.

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