SMALL MAMMAL POLLINATION IN *PROTEA WITZENBERGIANA*

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Protea witzenbergiana

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ABSTRACT

Protea witzenbergiana possesses some features common to that of therophilous *Proteas* in the Cape Floristic Region, such as a cup-shaped, downwards-hanging inflorescence surrounded by red involucral bracts, which emits a yeasty, musky odour. The flowering season occurs in the winter and the plants occur in small, localized and isolated stands in the Witzenberg fynbos. However, the species has never been investigated as to whether it is pollinated by small mammals. This study investigated whether the plant is rodent-pollinated, and if so to what extent by various species. Fieldwork was carried out over three days of live trapping, during and after the flowering season. Exclosure experiments were set up in order to assess seed set. Mammal droppings were collected, processed and pollen grains were counted. All small mammal species excepting one (*Otomys irroratus*) contained pollen grains in their faeces. *Dendromus melanotis, Mus minutoides* and *Aethomys namaquensis* were found to be the most important pollinators. The small mammal community showed a distinct change in size and composition after flowering season had ended, suggesting that the availability of nectar resources may be an important food supply to small mammals in the area. Implications of these findings could be relevant for conservation and co-evolutionary studies.

INTRODUCTION

Small mammal pollination (therophily) has been recorded in Australia, China, India, Malaysia, the Neotropics, tropical Africa and South Africa (Wiens *et al.,* 1979; Lumer, 1980; Rebelo & Breytenbach, 1987; Cocucci & Sersic, 1998; Wang *et al.,* 2008). Since the first paper written on non-flying mammal pollination in the south-western Cape by Rourke and Wiens (1977), therophily has been shown to be an important pollination syndrome in many South African Proteaceae, particularly in the Cape flora (Rourke & Wiens, 1978; Rebelo & Breytenbach, 1987; Fleming & Nicolson, 2002; Biccard & Midgely, 2009).

Pollination occurs when small mammals visit the flowering heads of plants in search of nectar rewards. While lapping the nectar, pollen is deposited on the rostrum of the animal and in this way is carried to neighbouring flowering heads, often up to 15m away (Wiens *et al.*, 1983). There are a number of floral morphological features common to these *Protea* species that suggest pollination by small mammals. These features include bowl-shaped heads borne on short, stout peduncles which grow at or near ground level; cryptic covering of heads by dense surrounding foliage; flexible styles with a nectar-stigma distance of 10mm (suitable for the rostra of visiting rodents); a yeastlike, musky odour and sucrose-rich nectar. In some plants, the whitish-coloured styles are surrounded by dark (purple or red-brown) involucral bracts. It has been suggested that this creates a "target effect", making the flower easier to spot in poor light (Wiens et al., 1983). Plants tend to have a winter-spring flowering season, coinciding with the peak of the breeding season of. Although a large number of *Protea* species with these characteristics occur, few have been thoroughly investigated as to whether they are indeed pollinated by small mammals (Wiens et al., 1983, Rebelo & Breytenbach, 1987 and Biccard & Midgely, 2009).

A number of rodent species in the Cape Floristic Region have been found to pollinate *Proteas*. These include *Otomys irroratus*, *Rhabdomys pumilio*, *Aethomys namaquensis* and *Myomyscus verreauxi* (Wiens et al. 1983, Biccard & Midgely, 2009). According to Biccard and Midgley (2009), *M. verreauxi* was largely responsible for the pollination of *Protea nana*. This rodent appeared to be the most adept climber out of these pollinating species –able to climb to the highest inflorescences of the plants. *R. pumilio* was also observed to climb well, and also contributed to the pollination of this species.

Another common feature of all therophilous *Protea* species is the relatively small, highly localized population distributions they occupy, which are often associated with specific soil types (Wiens et al., 1983). Therophilous species occupying the same area often have staggered flowering seasons. Rebelo and Breytenbach (1987) argue that this phenomenon has evolved in response to the generalist feeding habits and non-migratory behaviours of resident small mammals. The plants need to ensure that they produce sufficient flowers and nectar rewards to ensure visitation; competition between therophilous species would not allow for this.

This project focuses on a *Protea* species that has not yet been investigated in terms of potential small mammal pollination: *Protea witzenbergiana*. It is a sprawling shrub that grows up to 0.5 m tall and up to 3 m across. The inflorescences are cup-shaped, hang downwards from the stem and are surrounded by red involucral bracts. The flowerheads emit a yeasty, musky odour. The flowering season occurs in winter and spring, starting in May and ending in September. The plants occur in small, localized and isolated stands in the sandstone, Witzenberg fynbos which occurs in the Cederberg and Bokkerivier Mountains (Rebelo, 1995). Although this species has a floral morphology that is suggestive of small mammal pollination, it does not fall completely into the category of therophilous *Protea* species, as its flowers are not situated on the ground but hang downwards from about 20-30cm above the ground. Its distribution, although small, occupies a similar area to that of other bird-pollinated *Proteas* (Rebelo, 1995).

The aim of this project is to determine if *P. witzenbergiana* is indeed pollinated by small mammals, and to what extent. Another aim of this study is to establish which rodent species are most important to the plant with regards to pollination. In order to investigate these questions, field work will be done in the Witzenberg fynbos. Sherman live traps will be set out in order to get an idea of the number and species of small mammals present in the area. Since pollen is ingested by the animals when they groom and preen themselves (Wiens et al., 1983), the faeces will be analysed for the presence and abundance of pollen. This will indicate whether the rodents are visiting the inflorescences. In addition to this, flower seed set will be counted at the end of the flowering season in order to analyse the effects of rodent visitation on pollination.

Lastly, this study will look at the possible effects of therophilous *Protea* species on small mammal populations in the area. It has been the belief that small mammals do not depend highly on the resources offered by therophilous plants. The nectar rewards serve merely as a "sweet treat", and are not an important component of the rodents' diet (Wiens et al,. 1983). Therefore, the plant is ultimately more strongly affected by changes in rodent populations than the other way around. However, the co-occurrence of another possibly therophilous *Protea* species, *P. piscina,* in the area, may suggest otherwise. *P. piscina* begins flowering after *P. witzenbergiana*. This leads to the possibility that the distribution of therophilous plants, and the nectar resources they supply, may affect the population sizes and distributions of small mammals in the area. Small mammal populations during and after the flowering season of *P. witzenbergiana* will be compared, in order to investigate this question.

This investigation is expected to provide evidence of small mammal pollination in *P. Witzenbergiana*, due to the characteristic floral morphology and localized distribution of the species. Potential pollinators are *M. verreauxi* and *R. pumilio*, as these rodents are good climbers and would be able to reach the inflorescences that grow above the ground. It is also expected that small mammal populations will be affected by the availability of nectar resources in the area.

MATERIALS AND METHODS

Mammal trapping

Fieldwork was carried out within a small, dense population of *P. witzenbergiana* on a farm in the Cederberg, Western Cape (33°06'14.9"S, 19°20'93.5"E). Two sites were selected on the farm, the first being less densely populated than the second. Trapping was done using Sherman live traps baited with a mixture of peanut butter and rolled oats, and covered with an insulation layer to prevent cold-induced mortalities.

Two nights of trapping were conducted in the winter, during the flowering season. The first was carried out on 21st June, 2011 at the first site. Sixty traps were strategically set out in the close vicinity of *P. witzenbergiana* plants. Traps were set out in the early evening before sunset, and inspected the following morning. The captured animals were identified and all of their droppings collected in labelled Eppindorf tubes. The second night was carried out on 29th June, 20011 and followed the same procedure excepting the layout of the traps: Five transects were marked out 10 m apart. Ten traps were set up along each transect, 5 m away from each other, resulting in a total of fifty traps set out and an area of 0.7 ha covered.

A third night of trapping was conducted at the end of the flowering season on 21st September, 2011. The procedure and set up of traps was identical to that of the second night.

Exclosure experiments

The pollinator exclusion experiment was set up at the first site on 21st June, 2011. Ten plants were randomly selected as well as three immature flower buds of the same size and degree of maturity on each plant. In order to exclude any potential small mammal pollinators from reaching the inflorescence, one flowerhead was enclosed in a wire cage constructed of 13 mm chicken wire. The second flowerhead was enclosed by a wire cage covered in shade cloth in order to exclude all potential pollinators (including insects). The cages were secured with cable ties and a wooden pole, so as not to damage or weigh down the inflorescences. The third flowerhead was labelled as a control.

The inflorescences were removed and collected three months later, after the flowering season had come to an end. Each inflorescence was cut open and analysed for seed set.

Faeces treatment and pollen counting

Faeces were stored in a fridge with a few drops of 70% ethanol for preservation until they were processed. The entire faeces sample of each species was weighed, and then mashed using a stainless steel spatula end. The spatula end was thoroughly cleaned and rinsed between samples to prevent contamination. 70% ethanol was added to each sample in proportion to the weight, so as to ensure that each sample would be diluted to the same concentration (the ratio was 3ml ethanol to 1g faeces). The sample was then vortexed for three minutes to extract the light pollen grains which would float on the surface.

One drop (10 µl) of each sample was pipetted onto a microscope slide, with one drop of Aqueous safranine added to stain the pollen grains. Pollen grains were counted in the full field of view at 400X magnification, scanning the entire coverslip length (22 mm). This was repeated four times for each sample, enabling 8.2% of the coverslip area to be sampled. Total pollen counts were recorded for each sample.

Plant density counts

In order to assess the density of the *P. witzenbergiana* population, plants that occurred within a width of 2 m down a 50 m transect were counted. This was repeated for all the five transects at the second site that were set out for the mammal trapping. Also, the co-occurrence of the other potential therophilous *Protea*, *P. piscina* with *P. witzenbergiana* was evaluated. This was done by counting how many *P. witzenbergiana* individuals were within 5 m of *P. piscina* along a 50 m transect.

Data analyses

Due to the small and inconsistent sample sizes of each species caught, pollen count data were analysed using the non-parametric Kruskal-Wallis ANOVA by Ranks test was performed by Statistica 10 to test for significant differences in pollen counts between species. A post-hoc non-parametric multiple comparisons test was then done to see where the biggest differences lay (StatSoft Inc. 2011). Pollen-count data were also represented graphically as a bar graph, with one standard deviation added.

RESULTS

Mammal captures

After the first night of trapping on 21st June 2011, a total of 17 small mammals were caught out of 60 traps, yielding a trapping success of 30% (Table 1). Four species were caught on this night, the most common being the Namaqua rock mouse (*Aethomys namaquensis*), followed by the Cape rock elephant shrew (*Elephantulus edwardii*), the Verreaux's mouse (*Myomyscus* verreauxii) and lastly the striped mouse (*Rhabdomys pumilio*).

The second night of trapping on 29th June 2011 resulted in a total of 26 small mammals caught out of 50 traps (Table 1), yielding a very high trapping success of 52%. Seven species in total were caught at this site, including the four species previously caught. Others were the Cape vlei rat (*Otomys irroratus*), the Gray climbing mouse (*Dendromus melanotis*) and the Pygmy mouse (*Mus minutoides*). The most common species was again *A. namaquensis,* followed by *M. verreauxii* and *D. melanotis*).

The second trapping session conducted on 21st September 2011, yielded quite different results. Nine animals in total were caught out of 55 traps (Table 1), yielding a much lower trapping success of 16.4%. Five species were caught this time. The Cape spiny mouse (*Acomys subspinosis*) was new to this study and one of the most caught species. *A. namaquensis* was once again also the most caught species. One *R. pumilio, M. minutoides* and *O. irroratus* were also caught.

Table 1: Composition of mammal captures at site 1 and 2 during the June and September trapping sessions.

Species	**Night 1**	**Night 2**	**Night 3**
Aethomys namaquensis	8	11	3
Myomyscus verreauxii	3	5	0
Rhabdomys pumilio	2	2	1
Elephantulus edwardii	4	2	0
Dendromus melanotis	0	4	0
Mus minutoides	0	1	1
Otomys irroratus	0	1	1
Acomys subspinosis	0	0	3
Total	17	26	9
Trapping success	30%	52%	16.4%

Pollen counts

Protea pollen grains were counted in the faeces for each species caught on the two nights in June. Two animals caught on the second night –*D. melanotis* and *M. verreauxii* – did not produce enough faeces to sample, and were not included in the counts or analyses. The total pollen counts for all species caught on both nights were combined, and the mean values with standard deviations are shown in Figure 2.

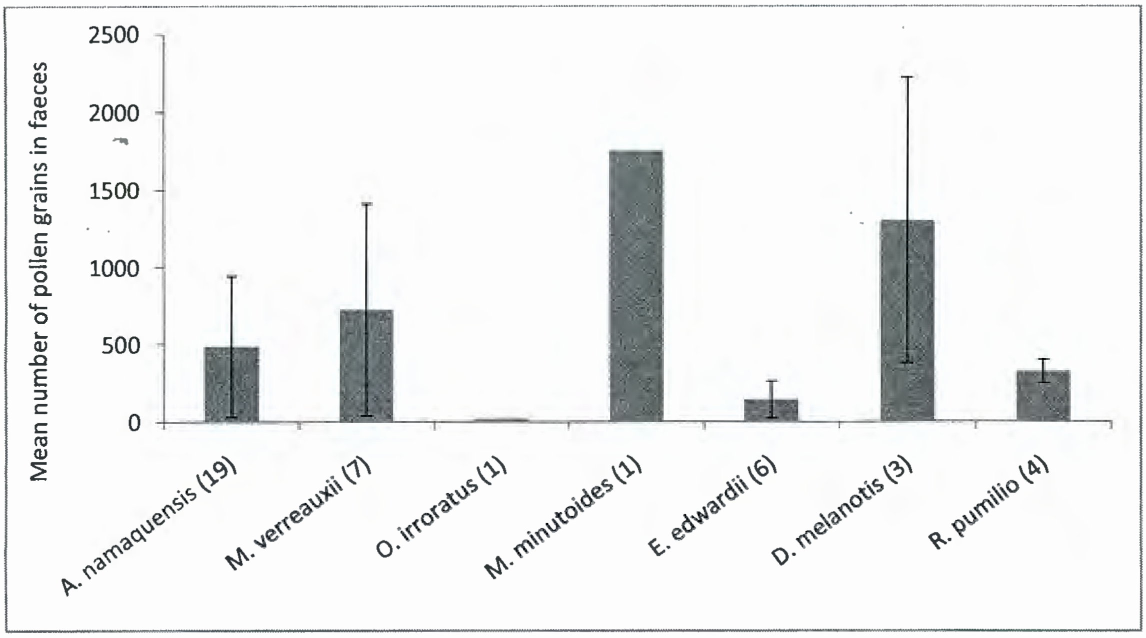

Figure 1: Mean number of *Protea* pollen grains counted in the faeces of all mammals caught during the June trapping sessions. A standard error bar has been added where applicable.

All of the species contained *Protea* pollen grains in their faeces, in varying quantities. The non-parametric Kruskal-Wallis test revealed that the pollen counts were significantly different for each species (H=12.27, N=39, p=0.016), the biggest difference being between *D. melanotis* and *E. edwardii* (H=12.27, N=39, p=0.017). *M. minutoides* had the highest mean value of pollen grains out of all the species at 1754 pollen grains. However, there was only one animal sampled, so this count may not be truly representative of the species. The next highest mean count was that of *D. melanotis* at 1302 pollen grains. This species also had the highest individual count of all the animals, with one *D. melanotis* having 2284 pollen grains. The next highest mean values are that of *M. verreauxii* and *A. namaquensis* respectively, although both of these species have high standard deviations and the counts varied *greatly*. Comparatively, *E. edwardii* and *R. pumilio* both showed more consistent counts and were lower than the previously-mentioned four. *O. irroratus* had the lowest of all, having only 20 pollen grains. Once again however, it is important to note that only one *O. irroratus* was sampled.

Exclosure experiments

Unfortunately, during the course of the study, a number of the exclosures were either lost or damaged by the farmer who ploughed through the transects. This left only four out of the original ten plants that had all three treatments. After cutting through the enclosed flowerheads, it was clear that they were too immature for the seeds to have set, therefore no conclusive evidence could be found to distinguish between the seed sets of the different treatments.

Plant density

From the five transects at site 2, 103 *P. witzenbergiana* individuals were counted, therefore averaging a density of 21 plants/100m^2. The counts of *P. witzenbergiana / P. piscina* co-occurrence transect revealed that 77.5% of *P. witzenbergiana* individuals occurred within 5 m of a *P. piscina* plant, therefore demonstrating that these two species strongly co-occur.

Other observations

While looking through the faeces samples, evidence of plant material, such has epidermal tissues, was apparent for all the species, including *E. edwardii.* This suggests that plant material is included the diets of all the small mammals caught in this study. Evidence of insect remains found in the faeces of *E. edwardii* and *M. minutoides* also suggests that these two species feed on insects and are not dependent solely on plant material for food.

DISCUSSION

The results of this study provide evidence that *P. witzenbergiana* is indeed pollinated by small mammals. This can be seen by the high number of pollen grains found in the faeces of almost all the animals that live amongst the plant population. As described in the introduction, pollen grains are ingested by the small mammals when they groom and preen themselves. Therefore, the presence of pollen in the faeces indicates that the small mammals in this study visited at least one inflorescence, thereby giving evidence for the potential of pollination.

From the faecal pollen grain counts and statistical analyses, it would appear that *D. melanotis* is the most important pollinator of the rodents, as all the animals of this species had relatively high pollen counts. This is not surprising given the remarkable ability of this rodent to climb - due to its long, prehensile tail and the long, opposable digits of its fore- and hind feet (Dieterlen, 2009). This would be an important skill to have, as the inflorescences are not situated on the ground but hang downwards from about 20-30 cm. *D. melanotis* would have easy access to the inflorescences compared to other rodents. There is no previous evidence of *D. melanotis* as a pollinator in the literature, however these rodents were observed to forage on the heads of non-flying mammal pollinated *Protea* inflorescences (Wiens *et al.,* 1983). *M. minutoides* would also appear to be an important pollinator given the relatively high pollen count. Perhaps the small size and weight of this animal allows it to climb to inflorescences without falling, enabling them to reach the nectar and pollen.

Despite the large variation in the pollen counts of *M. verreauxii*, this species also appears to be an important pollinator of *P. witzenbergiana.* A study done by Biccard and Midgely (2009) investigated the pollination syndrome of *Protea nana.* They conducted observations on the behaviour of a number of potential pollinating rodents, and found that *M. verreauxii* displayed remarkable climbing abilities and was even able to lick the nectar of *P. nana* inflorescences whilst upside down. Other observations, including tracing the path and visits of the animal using UV powder, added to the conclusion that *M. verreauxii* was a legitimate pollinator of *P. nana.* Therefore, it seems that this rodent is a significant pollinator of *P. witzenbergiana.*

A. namaquensis is possibly another species important for pollination, due to a number of the samples having relatively high pollen counts. Observations by Biccard and Midgely (2009) revealed that despite the poor climbing ability of this rodent due to its large size, it was interested in the nectar of *P. nana* inflorescences and was able to reach those which were close to the ground. These observations may also account for the rodent's behaviour and the resulting high pollen counts in this study. From the numbers of animals caught, it would appear as if the population of this species is large compared to the others'. Therefore, *A. namaquensis* may be important to *P. witzenbergiana* by virtue of their sheer numbers, despite the fact that they may visit the flowers less than other species on an individual level. The low pollen grain counts in some *A. namaquensis* samples may be due the individuals being caught early in the night, and not having a chance to visit a flowerhead. Or the animals may have been caught immediately before the traps were collected, allowing very little time for grooming and preening in the traps, and resulting in few pollen grains in the faeces.

The low pollen grain counts of the other three rodents are not surprising. *O. irroratus* was observed by Biccard and Midgely (2009) to show very little interest in *P. nana* inflorescences. It is a large rat, and would probably find much difficulty in climbing to reach the overhanging *P. witzenbergiana* inflorescences. *R. pumilio* is also a relatively clumsy climber and would only be able to reach a few inflorescences (Biccard & Midgely, 2009). *E. edwardii* is insectivorous, and was therefore not expected to be an important pollinator. However, it is known to feed extensively on seed, perhaps because of the low insect densities in fynbos (Nel *et al.*, 1980), and the plant tissue found in the faecal samples also suggested that this species may be prone to feeding on nectar. *E. edwardii* was found to be a potentially important pollinator of *Protea humiflora* (Fleming & Nicolson, 2002) and may be attracted to the insects found on the *P. humiflora* inflorescences. Recently, it has been found to be an important pollinator of the Pagoda Lily (*Whiteheadia bifolia*) in the Cederberg (Wester, 2011). However, these inflorescence are situated on the ground, which would indicate that once again, the climbing abilities of the various small mammals in this study seem to be a determining factor of the extent to which they are important for pollination.

Although the distribution of *P. witzenbergiana* in the Cederberg area is not very small, the high density recorded in these results is also evidence to support the hypothesis that they are rodent pollinated, as many other therophilous genera in southern Africa and Australia demonstrate this same feature. Wiens *et al.* (1983) argue that the small, highly localised populations of small mammal pollinated *Proteas* in the Cape, many of which occur in scattered, isolated habitats, provide advantages for non-flying mammal pollinators over birds. Small mammals are convenient pollinators to these plants, as they are ubiquitous to the area, available all year round (non-hibernating), do not migrate and are generalist feeders (Wiens et al., 1983). These characteristics are important for *Protea* species of localized and limited distribution, because it means that the animals will be attracted to nectar rewards all year round. Their continuous presence offers a reliable pollination service, and allows for varying phenologies of co-occurring *Protea* species (Wiens et al., 1983). The small mammals in this region are non-hibernating, non-migratory and are generalist feeders (Roberts, 1951) and would therefore be greatly attracted to the *Protea* nectar rewards – an ephemeral and highly restricted resource – and would therefore make reliable pollinators.

This implies that the plants are more dependent on the small mammals for survival than they are on the plants. However, the results in this study show a distinct change in the small mammal community during and after the flowering season. Breytenbach (1983) conducted trapping sessions in the sandstone fynbos of The Swartberg. He used the same method of transect layout and grid size as was used in this study and obtained a trapping success of only 8%. A survey done by Willan and Bigalke (1982) conducted similar trapping sessions but with an area of 2.4 ha. Their highest trapping success was only 27.6%. The highest trapping success of Biccard and Midgley's study (2009) was 21%. Therefore, it would appear that during the flowering season, the population density of small mammals amongst this stand of *P. witzenbergiana* is remarkably high, compared to other fynbos sites, as indicated by the trapping success rates of 30% and 52%.

After the flowering season had come to an end, trapping success was reduced to more than half, and a previously absent species, *A. subspinosis,* became the most dominant. These results clearly indicate a change in the population size and composition of the small mammal community. Fleming and Nicolson (2002) suggest that nectar and pollen supply a significant resource to small mammals , despite the geographically and temporal limitations of the resource. The sucrose-rich nectar of therophilous *Protea* species is a readily digestible energy source (Wiens *et al.,* 1983) and some rodent species (e.g., *A. namaquensis*) is able to meet all of its nitrogen requirements solely on a pollen and nectar diet (van Tets *et al.,* 2000). This evidence suggests that the nectar resources of *Protea* plants provide an important resource, and not merely a "sweet treat".

Studies have shown that small mammal populations can change and shift, depending on the season, as well as the post-fire stage of succession (Willan & Bigalke, 1982; Breytenbach, 1983). Fox *et al.*(1985) showed that small mammal species richness, density and diversity show great fluctuations depending on the post-fire successional stage in South African, Australian and American Mediterranean-type flora. This is evidence to suggest that the changes seen in the small mammal community composition in this study may be due to migratory movements. Since these changes occur between after the flowering season has ended, and nectar resources are low, these migratory movement may be in response to the availability of this important food resource.

P. piscina is a rhizomatous shrublet, with leaves coming out in tufts from the underground stem, and grows up to 1m. The flowerheads are cryptic, turban-shaped, have yellow or pink involucral bracts and are situated on the ground – a floral morphology typical of therophilous *Proteas* (Rebelo, 1995). This species flowers in the spring, soon after *P. witzenbergiana* stops flowering.

The co-occurrence of these two *Protea* species and their staggered phenologies, together with the distinct change found in the small mammal community, is evidence to support the possibility that the small mammals may depend more on the nectar resources supplied by these plants than previously thought. Pollen grains were found in almost all the small mammal species, some more than others, suggesting that almost all of them use the resources, and therefore pollinate the plant. The results would therefore suggest that *P. witzenbergiana* is pollinated by small mammals, at least partially, and that the mutualism is not restricted to a single species.

Further investigation, such as the observation of small mammal behaviour around *P. witzenbergiana* inflorescences, repetition of the exclosure experiments, and observations of possible bird and insect pollination, could strengthen the results of this study. They could also shed light onto the strength and dependence of both plant and animal on the mutualisms discovered here. The findings could provide important insights into the conservation of both the *Protea* species, and small mammal species, especially if the small mammals are more dependent on the distribution of *Proteas* and the resources they supply.

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