# Is the distribution of *Liparia* determined by disturbance or mutualism?

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## Abstract

I investigated whether the locally endemic *Liparia parva* was influenced in its distribution by the distribution of its principal pollinator *Acomys subspinosus* or by rocks acting as buffers against disturbance by fires. Sampling was carried out at Redhill on the Cape Peninsula (South Africa) during the winter of 2010 by trapping rodents with Sherman live and PVC traps, performing vegetation analyses and analyses of its relationship with rocks. My results show no link between *Acomys* presence and rocks, *Acomys* and *Liparia* co-occurrence and flower visitations as a function of distance to rock; however the absence of rocks was associated with the absence of *Liparia* and an increase in rocks (of up to 1 m height) was associated with an increase in *Liparia* abundance. This suggests that the distribution of *Liparia* is not influenced by *Acomys* and that *Liparia* is restricted to areas with rocks. I therefore concluded that the distribution of *L. parva* was determined not by its mutualism, but by rocks as a buffer against disturbance.

## 1. Introduction

Four principal drivers of community biogeography have been identified in the literature, namely environmental factors, competition, disturbance and mutualisms (Cowling et al. 1997). Of the environmental factors, altitude-aspect gradients, coast-to-interior gradients, west-to-east gradients, (Campbell 1983) soil depth, texture, fertility, pH, winter radiation loads and rock cover were most prominently cited as explaining community patterns in fynbos (Cowling 1992, Richards et al. 1995). Further influences on distribution are disturbance factors such as catastrophic events (e.g. droughts) and (for the fynbos most importantly) fire (Cowling et al. 1997). Lastly, mutualism has been established to be determining of the biogeography of fynbos, most notably through seed dispersal and pollination (Bond et al. 1991, Cowling et al. 1997). Since all of these factors directly influence communities and their members it is logical to assume that they have some impact on the species within these communities. This may be of specific interest when investigating the biogeography of endemic species with very limited distributions which may be due to these factors.

One such species is a locally endemic member of the *Fabaceae*; *Liparia parva* can only be found in a very limited distribution on the Cape Peninsula and has recently received attention due to representing the first known member of its family to be pollinated by a rodent (Letten and Midgley 2009). *L. parva* is conspicuously restricted to rocky outcrops, and its distribution is limited to hills and mountains whose soils were formed from Table Mountain Group sediments. It is also a re-sprouting species (pers. Comm. Midgley 2010). These soils are highly deficient of exchangeable bases and extractable phosphorus and this has been shown to be correlated with high floral endemism (Kruger 1979, Cowling et al. 1997).

The genus *Liparia* consists of some 20 species, which are all endemic to the region (Schutte 1997). Although there are great differences in inflorescence morphology between these 20 species *L. parva* is obviously adapted to rodent pollination by having pale yellow geoflorus inflorescences and by flowering in winter (from July to August) (Schutte 1997). Rebelo and Breytenbach (1987) found that many rodent pollinated plants in the Cape Floristic Region flower in winter as the energy rich nectar would attract rodents during this time when insects are inactive. Following this obvious predisposal towards rodent pollination, Letten and Midgley (2009) established that the Cape spiny mouse *Acomys subspinosus* may be the principal pollinator of *L. parva*. Pollen in the scats of *A. subspinosus*, reductions in seed set during exclusion experiments and observations of non-destructive foraging on *L. parva* inflorescences supported their conclusion. Small numbers of seed set in enclosed inflorescences furthermore suggested that *L. parva* is an out-crosser with some selfing taking place in very mature inflorescences (Letten and Midgley 2009); they therefore surmised that rodents were critical for the fitness of this species.

Studies by Johnson *et al.* (2001) and Fleming and Nicolson (2002) have previously illustrated the nocturnal *A. subspinosus* to be an important pollinator of other species in the Cape; it has also been shown to be a significant seed disperser (Midgley *et al.* 2002). Therefore *Acomys* might be a keystone species in the area. However, besides these isolated findings, not much is known about the ecology and behaviour of *A. subspinosus* (Skinner and Chimimba 2005), though Wiens et al. (1983) found that it has a home range of 35.0-47.5 metres, and some anecdotal evidence associates it with rocky habitats (pers. Comm. Midgley 2010).

Having identified *L. parva's* principal pollinator, to what extent is the distribution of the plant linked to its pollinator?

Although, studies have traditionally focused on plant fecundity being limited by resources, numerous studies have established that it may alternatively be regulated by the level of pollinator availability (Ackerman and Montalvo 1990, Willson 1991, Wilson 1994). Johnson (1997) for example found that pollen limitation was high in the fire prone fynbos due to a naturally low availability of pollinators (including insects and birds) and reductions in pollinator populations after fires. Wiens et al. (1983) for example found that a number of *Protea* species being pollinated by non-flying mammals all shared characteristically small and isolated populations, as does *L. parva*.

Another factor that may influence the distribution of *Liparia* is disturbance, in this case fire. Rocks have been shown to protect plants from fires, thereby creating fire refuges that may enable *L. parva* to grow more vigorously (i.e. more flowers) and thereby maintain its limited distribution on or near rocky outcrops only (Midgley et al. 1998). This means plants would have progressively less flowers as one moves away from rocks. Secondarily, rocks could have an indirect effect on plants by providing habitat for *Acomys*. Resultantly, the following question was asked in this study: Is the distribution of *L. parva* determined by its rodent pollinator or by rocks?

This will be investigated by exploring the relationships between rocks and *Acomys*, rocks and *Liparia* abundance and vigour, and *Acomys* and *Liparia*.

The aim of the study is to establish the determining factor(s) of its distribution to further our knowledge about its biogeography; and the Hypotheses are:

$1H_1$: The distribution of *L. parva* is linked to the distribution of *A. subspinosus*.

$2H_1$: The distribution of *L. parva* is linked to the presence of rocks.

## 2. Materials and Methods

To determine the distribution of *Acomys*, trapping was carried out during the 16-19th of June, 26-30th of July and the 2-5th of August 2010 and visitation rates were monitored between the 3rd and 26th of August 2010. All field work was carried out on the cape Peninsula at Redhill (34°11▯S, 18°24▯E, elevation 250 metres) near Table Mountain National Park, South Africa. The area supports a *Liparia* population of about 1 plant/5 $m^2$ (Letten and Midgley 2009). Traps were baited with rolled oats, vegetable oil, peanut butter, raisins and bacon and were checked in the morning, before sunset and occasionally during night times.

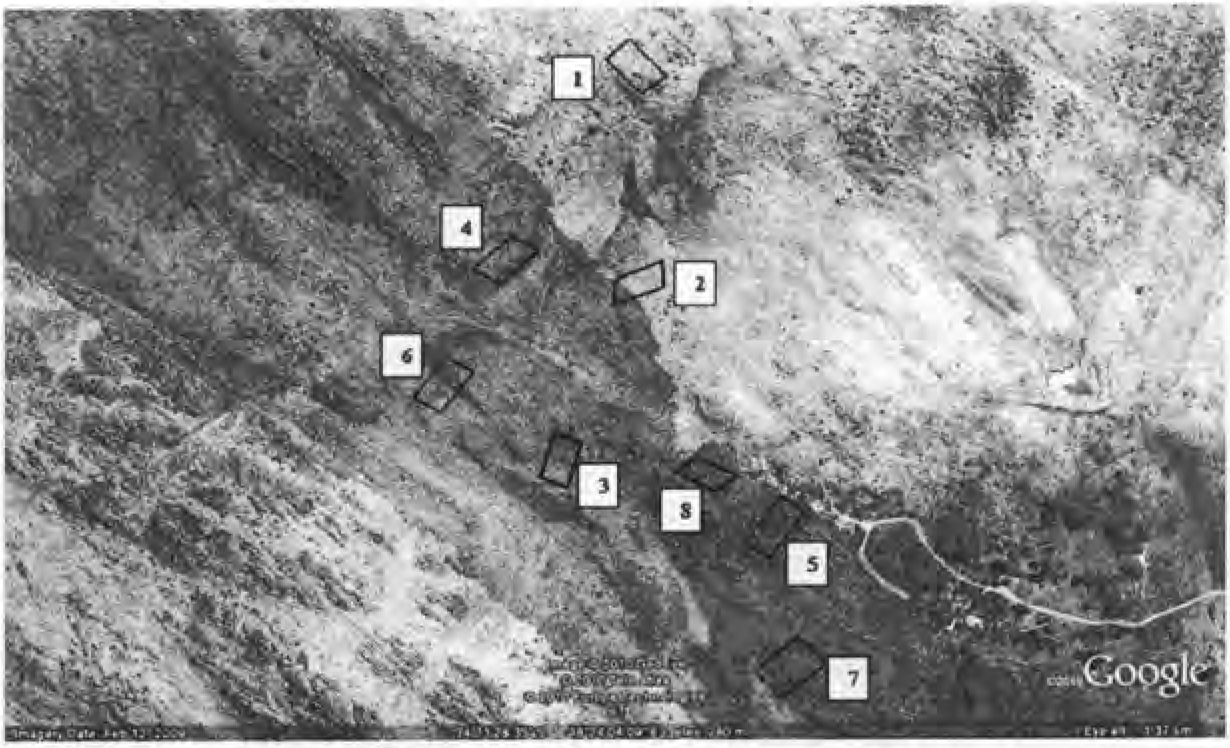

Fig. 1 Map of the study sites 1-8; note the lighter areas which burnt in 2008 and contain grid 1 and 2

*First trapping session*

Sherman live traps were set out at 5X5 m intervals at grid locations 1-4. A cotton ball was placed in each trap to improve insulation during the night. Trapped animals were weighed, sexed and marked with permanent marker pen, fur clipping, ear marks or Ultra Violet (UV) dust to mark of their local movement patterns. All animals were immediately released at their trapping location.

*Second trapping session*

During the second session, the trap spacing was increased to 10X10 m to allow for the large distances travelled by the rodents and an additional 3 grids were set out to increase the sample size. During this session both Sherman live traps and PVC traps were used. A cotton ball was placed in each trap and Sherman traps were wrapped in Styrofoam to improve insulation during the night. Trapped animals were processed as before, with the addition that some were injected with PIT tags which could be read with a PIT tag reader at recapture (FS2001F-ISO Reader from Biomark, Inc.); this method allowed decreased handling times at recapture.

*2.1 UV trailing*

To investigate movement patterns of the rodents UV trails were followed at night with UV torches and were marked with cotton string. The resultant paths were mapped during the day to get an idea of the movements of *Acomys*.

### *2.2 Vegetation analysis*

To determine relationships between *Liparia* (abundance and vigour) and rocks, vegetation analyses were carried out for grids 2, 4, 5 and 8. The grids were divided into 5X5 m plots, within which the number and size classes of rocks and *Liparia* were recorded. *Liparia* size was based on the number of inflorescences (representing their vigour) and divided into 4 classes which approximately equally divided the range of inflorescence numbers observed in plants. Rock classes were determined similarly, dividing the observed size range into 4 equal intervals. The class specifications were as follows:

Table 1. Class divisions of rocks and *Liparia*

| **Rocks** | | ***Liparia*** | |
|---|---|---|---|
| Class | Height of rock (cm) | Class | No. of inflorescences |
| 1 | 0-50 | A | 0 |
| 2 | 50-100 | B | 1-5 |
| 3 | 100-150 | C | 6-10 |
| 4 | >150 | D | >10 |

Mann Whitney U-tests and quantile regressions were performed on *Liparia* abundance and rock data and Box and Whisker plots compiled to represent the Mann Whitney U-test results visually. 2X2 $Chi^2$ contingency tables were used to test for a relationship between the absence of rocks and *Liparia*, *Acomys* and rocks, and *Acomys* and *Liparia*.

### *2.3 Visitation rates*

To determine the link between rocks as a habitat for *Acomys* and pollination in plants, fifteen plants of size classes C and D were selected and the number of flowers visited was recorded at weekly intervals for four weeks. Visitation was determined as described by Letten and Midgley (2009) and visited inflorescences were marked with horticultural marking tape. The distance to the nearest rock of different size classes was also recorded for all plants. Regressions were plotted for number of visitations versus distance to rocks.

## 3. Results

### 3.1 Movement patterns

A total of 61 *Acomys* were captured with 23 separate individuals (and 6 mortality cases); the maximum overnight distance moved by an individual was 301 metres (distance between the two capture points), and this was along a rocky ridge. Anecdotal evidence from the UV mapping also suggests that *Acomys* preferably moves alongside or underneath rocks wherever possible, and that it utilises both burrows located underneath rocks and in the open. Multiple individuals also used the same paths when crossing open terrain.

Table 2. Total number of *Acomys* captures for both trapping sessions; note the low capture numbers for the two burnt grids (1 and 2)

| **Grid Number** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** |
|---|---|---|---|---|---|---|---|---|
| ***Acomys* Captures** | 1 | 1 | 11 | 6 | 18 | 4 | 8 | 10 |

#### *3.2.1 Liparia abundance and rocks*

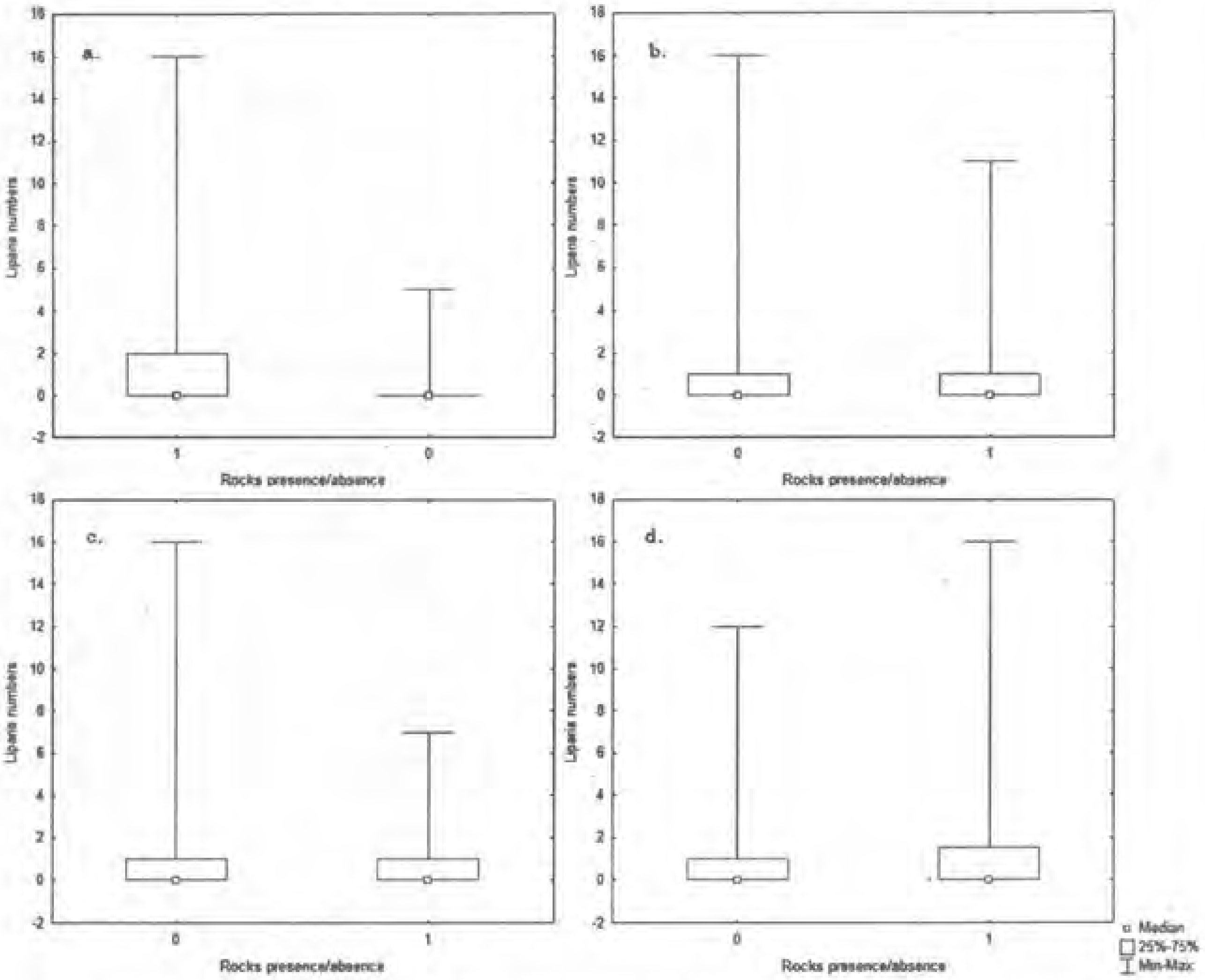

Fig. 2 Box and Whisker plots of Liparia numbers versus rock presence/absence for rock classes 1-4 (plots a., b., c., d. respectively); burnt and unburned grids are combined as *Liparia* is a resprouter, with its abundance not being negatively influenced by fire as individuals resprout after fire without dying

The Mann Whitney U-tests in fig. 2 yielded the following: a. $p = 0.01$, $Z = 3.04$; b. $p = 0.40$, $Z = -0.83$; c. $p = 0.46$, $Z = 0.75$; c. $p = 0.93$, $Z = -0.09$. This shows that there is only a significant difference between the numbers of *Liparia* for the presence/absence of rock class 1.

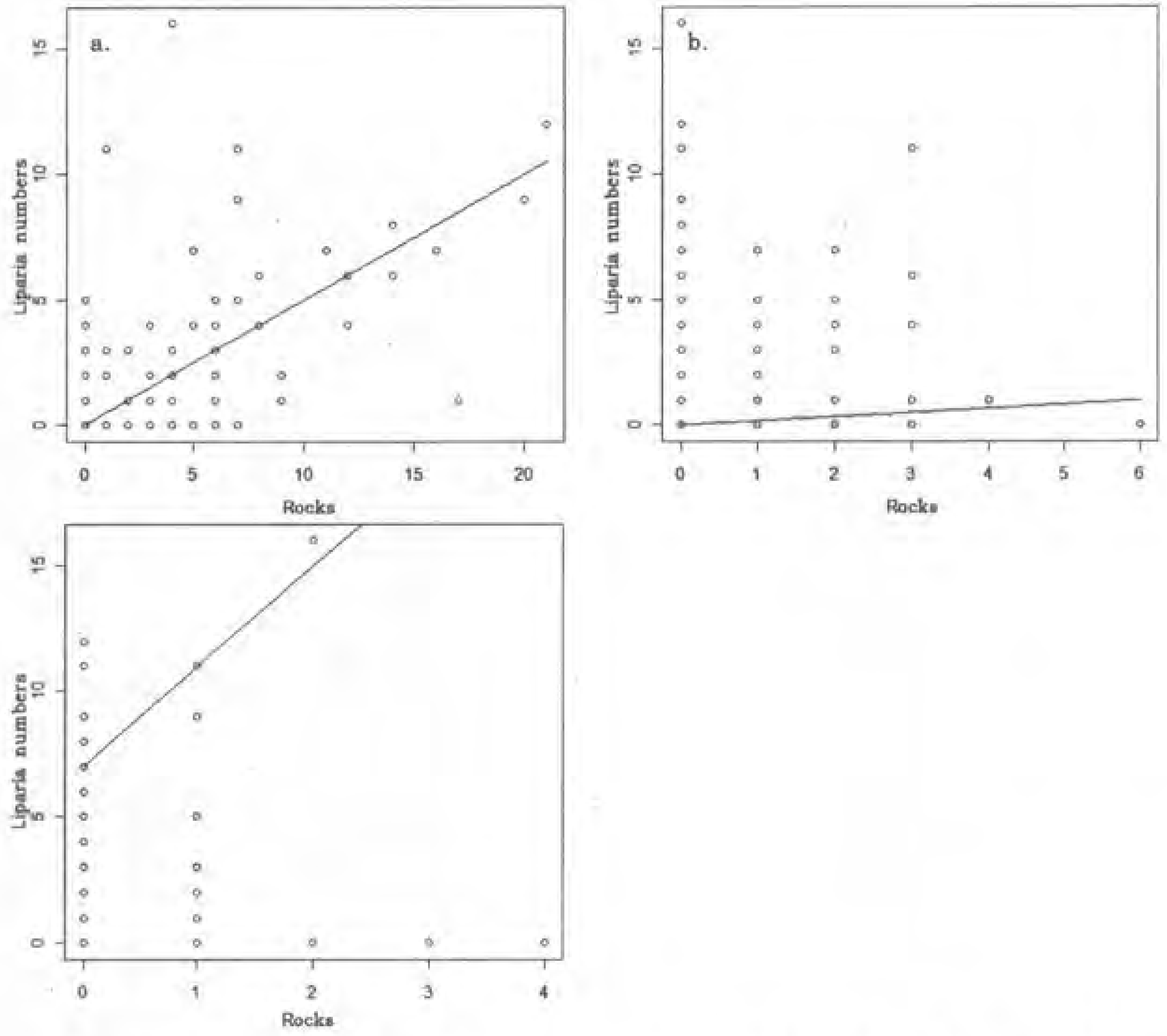

Fig. 3 Quantile regression trend lines on plots of *Liparia* numbers vs. rocks for rock classes 1, 2, 4 (plots a., b., c. respectively); no significant trends were found for rock class 3

The lines in plots a-c represent the trends as calculated by the quantile regression for the 70th, 50th and 95th percentile respectively. This means that approximately 70% of the data have been ignored for rock class 1 and so on. Quantile regressions were used here to eliminate the possible confounding effect of an unmeasured variable (such as environmental gradients) on trends in the data set related to the measured variable (for details see Cade et al. (2005)).

The quantile regression is used to find trends in subsets of data, in this case removing all data points were rocks were present but no *Liparia*. The test yielded the following: a. $t = 8.55$, $p < 0.01$, $y = 0 + 0.5x$; b. $t = 10.24$, $p , 0.01$, $y = 0 = 0.17x$; c. $t = 2.22$, $p = 0.03$, $y = 7 + 4x$.

### *3.2.2 Liparia absence versus rock absence*

Table 3. Frequency data of *Liparia* and rock absence/presence

| | **Liparia** | **No Liparia** |
|---|---|---|
| **No Rocks** | 3 | 47 |
| **Rocks** | 34 | 85 |

The 2X2 $\text{Chi}^2$ contingency table above yielded a p value of 0.0012 (df = 1), showing a statistically significantly higher occurrence of *Liparia* in plots with rocks than in plots without them.

### *3.2.3 Liparia vigour and rocks*

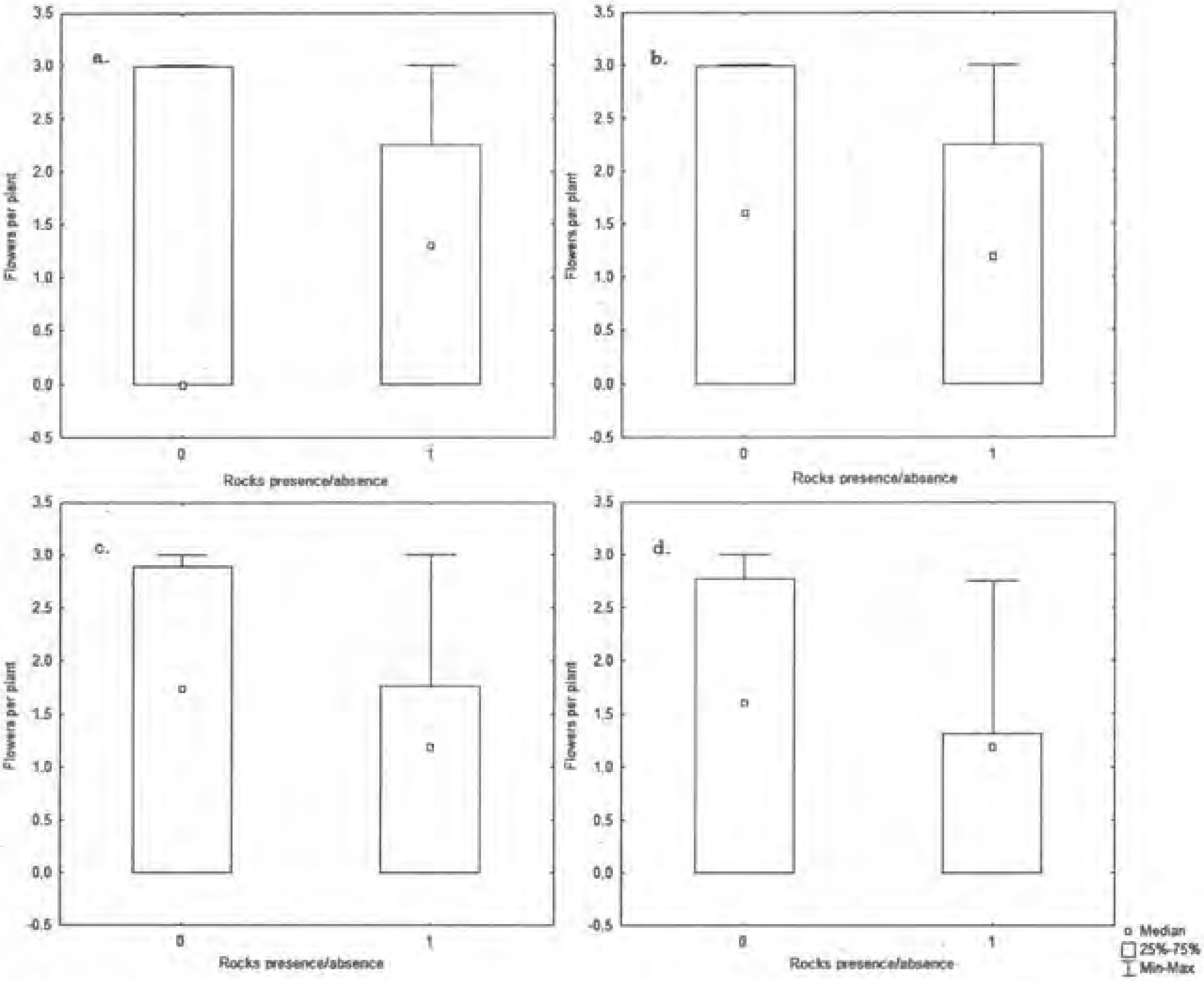

Fig. 4 Box and Whisker plots of the number of flowers vs. rock presence/absence for rock classes 1-4 (plots a-d respectively) in unburned grids 4, 5 and 8

Fig. 4 and fig. 5 are of unburned and burnt grids separately as recent fires would have a negative effect on plant vigour. The Mann Whitney U-test statistics for fig. 4 were: a. $p = 0.79$, $Z = -0.27$; b. $p = 0.49$, $Z = 0.70$; c. $p = 0.31$, $Z = 1.01$; d. $p = 0.33$, $Z = 0.98$. This shows no significant relationships between *Liparia* vigour and rock presence or absence.

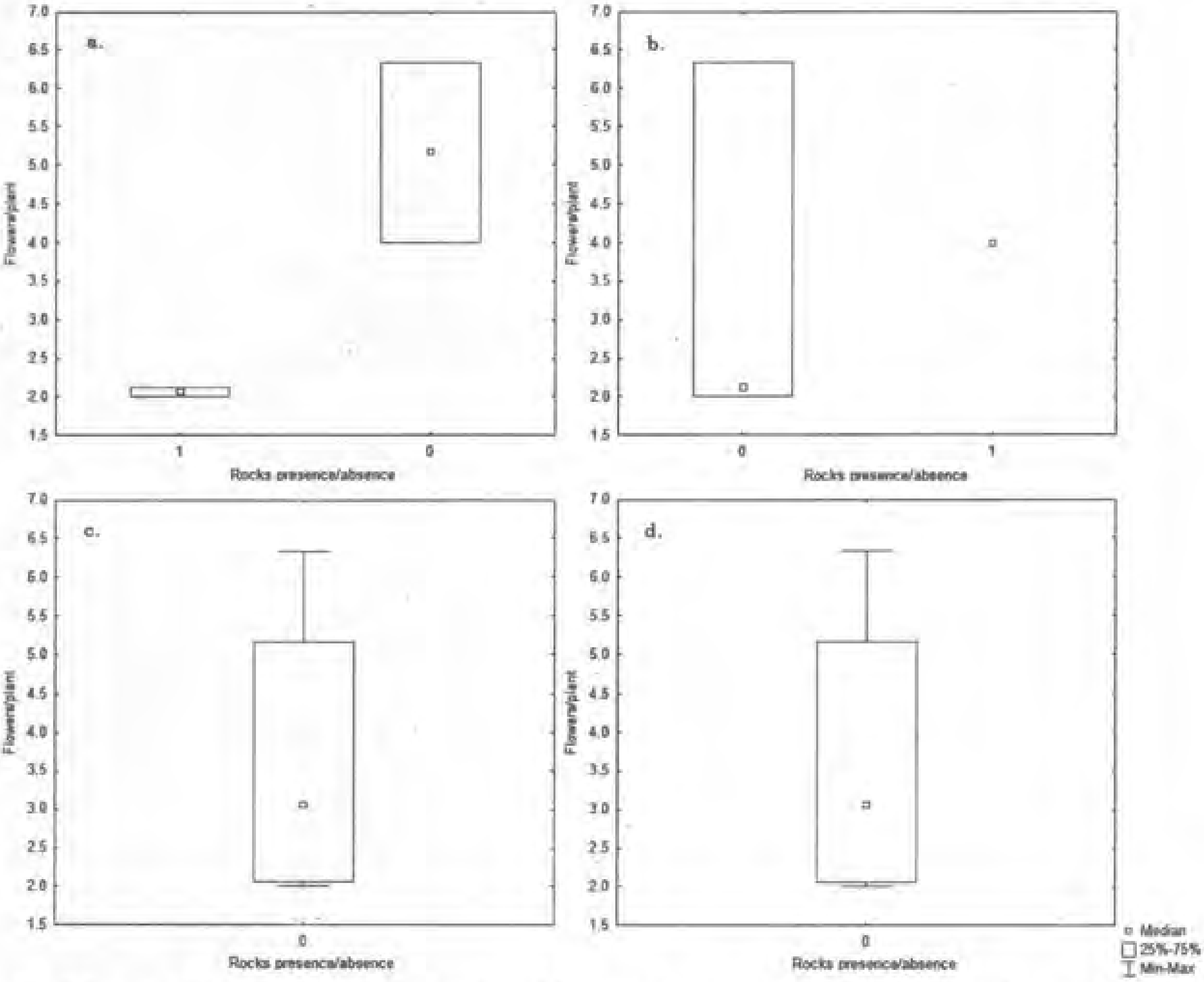

Fig. 5 Box and Whisker plots of the number of flowers versus rock presence/absence for rock classes 1-4 (plots a-d respectively) in the burnt grid (2); no class 3 and 4 rocks were found, hence their absence in plots c. and d.

The corresponding Mann Whitney U-tests showed the following: a. $p = 0.25$, $Z = -1.16$; b. $p = 1.00$, $Z = 0.00$; c. $p = 1.00$, $Z = 0.00$; d. $p = 1.00$, $Z = 0.00$. This shows no significant links between rock presence/absence and *Liparia* vigour for the burnt grid.

### *3.2.4 Acomys and rocks*

Table 4. Chi$^2$ test results for unburned grids (4, 5 and 8), showing no significant dependence of *Acomys* on rocks

| | Class 1 | | | Class 2 | | | Class 3 | | | Class 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** |
| **Acomys** | 20 | 2 | 0.55 | 14 | 8 | 0.89 | 12 | 10 | 0.48 | 9 | 13 | 0.32 |
| **No Acomys** | 36 | 6 | | 26 | 16 | | 19 | 23 | | 12 | 30 | |

Table 5. Chi$^2$ results of *Acomys* versus rocks for the burnt grid (2), showing that *Acomys* only depends on the presence of class 2 rocks; N/a indicates invalid data entry for a Chi$^2$ test due to zero values for *Liparia*

| | Class 1 | | | Class 2 | | | Class 3 | | | Class 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** | **Rocks** | **No Rocks** | **Chi$^2$ p value** |
| **Acomys** | 0 | 1 | 0.36 | 1 | 0 | 0.00 | 0 | 1 | N/a | 0 | 1 | N/a |
| **No Acomys** | 8 | 9 | | 0 | 17 | | 0 | 17 | | 0 | 17 | |

### *3.2.5 Acomys versus Liparia*

Table 6. Chi$^2$ results for *Liparia* versus *Acomys* for the unburned grids (4, 5 and 8); showing no dependence of *Acomys* on *Liparia* or vice versa

| | Category A | | | Category B | | | Category C | | | Category D | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** |
| **Acomys** | 10 | 12 | 0.57 | 6 | 16 | 0.49 | 2 | 20 | 0.78 | 1 | 21 | 0.64 |
| **No Acomys** | 16 | 26 | | 15 | 27 | | 3 | 39 | | 1 | 41 | |

Table 7. Chi$^2$ results for *Liparia* versus *Acomys* for the burnt grid (2); showing a relationship between *Acomys* and *Liparia* plants of Category C only

| | Category A | | | Category B | | | Category C | | | Category D | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** | **Liparia** | **No Liparia** | **Chi$^2$ p value** |
| **Acomys** | 0 | 1 | 0.72 | 1 | 0 | 0.05 | 1 | 0 | 0.00 | 0 | 1 | 0.80 |
| **No Acomys** | 2 | 15 | | 3 | 14 | | 1 | 16 | | 1 | 16 | |

### 3.3 *Liparia* visitation versus distance from rocks

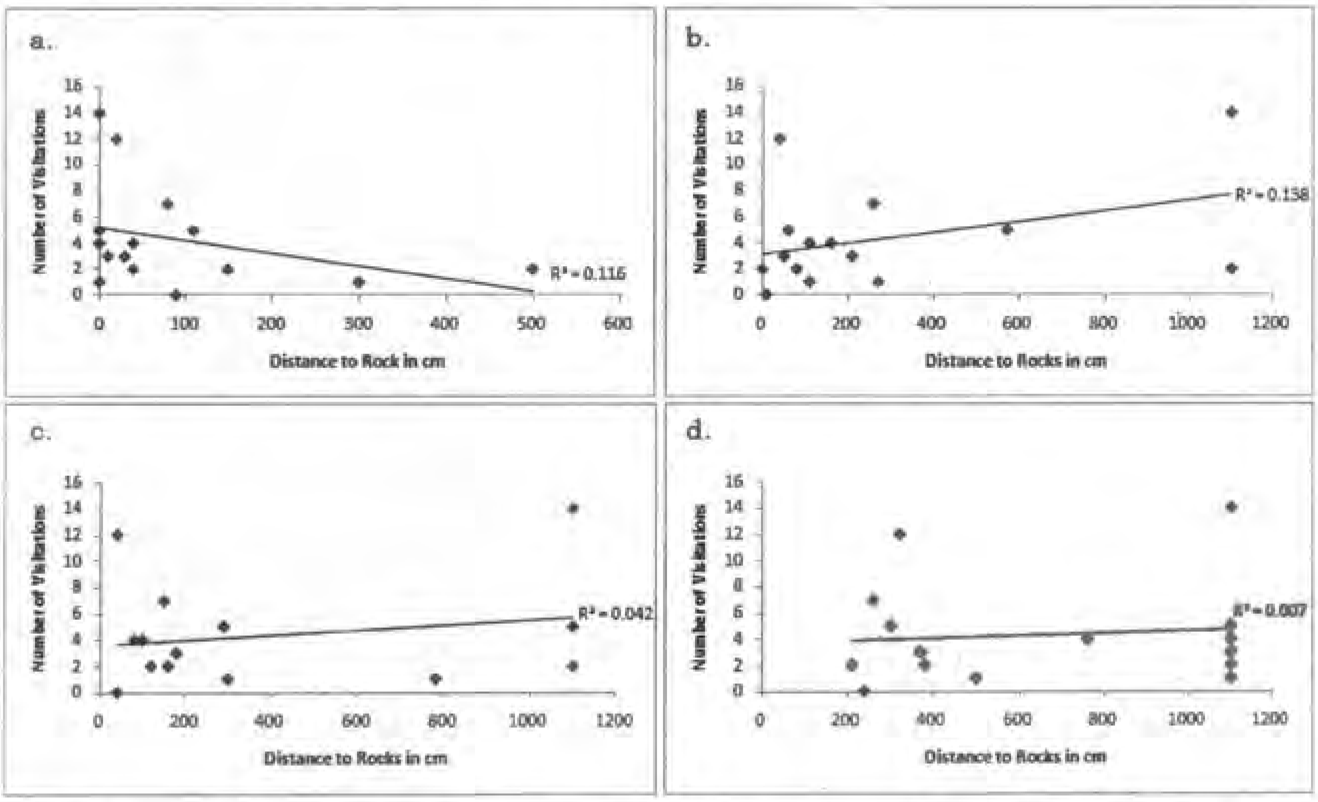

Fig. 6 Regression plots of visitations vs. distance to rock classes 1-4 (plots a-d respectively); p values: 0.21, 0.17, 0.46, 0.77 respectively (df = 1.13)

## 4. Discussion

### *4.1 General observations*

The UV results were in support of anecdotal evidence that *Acomys* prefers rocky habitats. Also conspicuous was the large difference between rodent captures in burnt and unburned grids with the burnt grids being largely devoid of rodents. One individual that was caught in grid 1 was recaptured in grid 2 the following day. This indicates that these two captures in the burnt grids may be accountable to rodents in transit from unburned sites. This is supported by my finding that *A. subspinosus* could move up to 301 m per night and by van Hensbergen et al. (1992) who observed lower population numbers after fire which was related to decreased live cover and cover density. The high mortality rate of about one quarter of the population was probably due to repeated recapture of these individuals (up to 4 times; leading to stress), clogging of the lungs during dusting with UV powder or clogging of the stomach with UV dust after grooming. As UV trails were only useful to track animals for approximately 20-30 m and did not reveal conclusive movement data it is recommended to limit its use as it may be the cause of an increased mortality rate.

### *4.2.1 Rocks and Liparia abundance and occurrence*

The $Chi^2$ tests showed that only class 1 rocks led to significantly different *L. parva* numbers. For rock classes 1, 2 and 4 the quantile regression suggested that 70%, 50% and 95% of the data respectively (comprised of all plots with rocks but no *Liparia*) had to be ignored in order to find significant trends. To disregard the zero readings for *Liparia* abundance in this method is possible as the lack of *L. parva* at sites with rocks may be due to its overall rare occurrence in the landscape. However, as the $Chi^2$ test did account for all those zero readings it may not be able to show significant trends in subsets of the data as can the quantile regression, therefore it will not be discussed further.

Rock class 4 only yielded a significant trend at the removal of 95% of its data and was therefore strongly influenced by the single outlier (see fig. 3). Only incorporating 5% of the data may be statistically questionable and therefore I will disregard this result. Thus only the increasing abundance of rocks up to a height of 1 m led to an increased *L. parva* abundance, possibly through shelter against fire or by providing habitat for the pollinating rodent.

However, the results show a significant general association of *Liparia* occurrence with rocks (see table 3). Although this does not quantify what type of rocks as above, it suggests that *L. parva* presence is rare in the absence of rocks. This underlines previous findings that *Liparia* is associated with rocky outcrops and shows that even at the small sub-plot scale (5X5 m) the absence of rocks implies the absence of these plants and supports the findings above. It also supports $2H_1$ by showing that the occurrence of *L. parva* is related to the co-occurrence of rocks.

### *4.2.2 Liparia vigour and rocks*

No significant difference in the number of *Liparia* was found when compared to the presence or absence of rocks for burnt and unburned grids alike. These results seem to suggest that at a 5X5 m sub-plot scale, the mere presence of rocks is not enough to significantly increase flowering of the plants. Other environmental factors or competition may be acting on the plants and may be more dominant than the presence of rocks as a protecting agent from disturbance.

### *4.2.3 Acomys and rocks*

No significant association between *Acomys* and rocks was found for the unburned grids and in the burnt grid only the absence of rock class 2 was significantly related to the absence of *Acomys*; however this was based on a single *Acomys* capture and may thus be regarded as statistically insufficient. Although this seems to suggest the absence of any direct link of *A. subspinosus* to rocks, the analysis is based on vegetation mapping at sub-plots of 5X5 m, which may be too fine a scale and may not reach far enough away from rocks due to the extensive movements of rodents (up to 301 m per night). Vegetation analyses at 20X20 m may yield stronger results indicating the otherwise observed association of *Acomys* with rocks.

### *4.2.4 Acomys and Liparia co-occurrence*

The only significant link was between Acomys and *L. parva* of category C in the burnt grid. This means that largely there appears to be no association of the rodent with *Liparia* plants in the grids, suggesting that *Acomys* does not solely depend on *Liparia* as a food source. Such dependence would otherwise have yielded a close link between *Acomys* captures and *Liparia* abundance. In the light of the large distances that some animals were able to move this result is not surprising, as this would enable *Acomys* to exploit a variety of plant food sources.

### *4.3 Visitation*

No significant trend in visitation was found away from rocks. However, the data suggest that most visitations occur within 4 m of rocks (see fig. 6) and the small $R^2$ values may be biased by a few outliers due to the small sample size ($n = 15$). One individual had 14 visitations and this in particular may have thrown off the analysis. It seemed that in the event of visitation, a plant is likely to have multiple of its flowers visited and therefore a single passing rodent may have caused the outlying visitations in the one individual. On the grounds of these findings, it is unclear whether visitations were significantly higher closer to rocks and that *Acomys* thereby would influence *Liparia's* distribution.

### *4.4 Conclusion*

My findings show an association between *Liparia parva* and rocks of up to 1 m height, a clear absence of *Liparia* in the absence of rocks, no link between the vigour of *Liparia* and rock presence, no link between *Acomys* and rocks and Liparia occurrence and generally higher visitation rates within 4 m of rocks than further away.

My study therefore suggests that small rocks protect *Liparia* from fires to increase its abundance but not its vigour; that *Acomys* is not strictly associated with rocks or *Liparia*, that flower visitation was not influenced by distance to rocks and therefore was not indirectly related to *Acomys*.

In conclusion, findings on *Acomys* did not display direct effects on the distribution of *Liparia* and only small rocks caused higher *Liparia* survival which could explain its association with rocky outcrops in the landscape. Therefore, the distribution of *L. parva* is not determined by a pollinator limitation but a disturbance factor.

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