IS LOCAL PLANT EXTINCTION A PRODUCT OF MUTUALISM BREAKDOWN?

(A case study of the Namaqualand spring flora)

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ABSTRACT:

A mutualism-centred risk assessment model, proposed by Bond (1993), was used to predict which plant species are vulnerable to extinction in the absence of insect pollinators. The predictions of this model were then compared with actual plant species compositions between adjacent disturbed and undisturbed sites in a Namaqualand flowering community. It was found that autogamous annuals were at the lowest risk of extinction and were consequently abundant in disturbed lands. Geophytes were completely eliminated by ploughing, however, the cause of their local extinction is not necessarily due to mutualism breakdown and may be explained by a lack of seed banks. The model was shown to be useful for predicting distribution patterns for annuals. However, further studies of seed banks, germination cues and colonisation success are necessary to make predictions for the geophytic species. The study illuminated the fact that both plant and associated insect species diversity decline rapidly in disturbed areas and that the elimination of insects, by ploughing, may lead to extensive loss of plant species.

1. INTRODUCTION

A central theme of conservation biology is understanding extinction processes and thereby elucidating the requirements for species persistence (Shaffer, 1990). A plethora of theories and models have been generated to predict species extinctions, in fragmented and anthropogenically disturbed areas. However, most of these theories (eg. Island biogeographic theory - MacArthur and Wilson, 1967; and population vulnerability analyses (PVA's) - Gilpin and Soule, 1986) are based on zoological principles and invoke population sizes and demographic uncertainty as the primary causes of extinction. These theories do not incorporate the implications of plant longevity and seed banks for species persistence, nor do they investigate the importance of biological interactions amongst species.

The disruption of mutualisms at pollination and seed dispersal stages; has recently been advanced as one of the most threatening consequences of fragmentation to neotropical forests (Bawa, 1990). Although only a few published studies have addressed this problem (Jennersten, 1988; Aizen and Feinsinger, 1994). Janzen (1987) has eloquently drawn attention to the extinction of "ecological interactions" in tropical forests as a result of habitat transformation. Plants are involved in a variety of pollination and dispersal mutualisms. Most reproductive mutualisms involve facultative relationships between an assemblage of interacting plant and animal species (Howe, 1984; Bawa, 1990; Horvitz and Schemske, 1990). Although obligate reproductive mutualisms do exist, these are relatively rare eg euglossine bees and orchids and fig wasps and figs.

Bond (1993) has recently attempted a new approach to predicting the risk of plant extinction, which explicitly includes the importance of pollination and dispersal mutualisms. This risk assessment focuses around three key concerns: 1) the probability of a mutualism failing due to the demise of mutualist partners 2) the degree of reproductive dependence on mutualism (facultative or obligate) and 3) the importance of seeds in the demography of the plant.

Insect diversity and abundance is known to decrease with decreasing habitat size and heterogeneity (Klein, 1989). The persistence of a plant species, in the absence of its insect visitor is dependant on the strength of the plant-pollinator interaction (Janzen, 1987). If a plant is morphologically adapted for specialist pollination ie dependant on one to a few closely related species, then the loss of this insect may result in local extinction of the plant species. Such extinction is only possible if the plant is short-lived and dependant on seeds for survival. Whereas long-lived resprouting species can persist even in the absence of specialist pollinators. If, however, a plant is visited by a set of generalist insects (which feed at flowers from many plant species), then the loss of an insect pollinator will not necessarily result in the extinction of the associated plant species.

Plant species which are self-pollinating: autogamous (facultatively autogamous), or cleistogamous, and apomictic plants will obviously not be at risk of extinction in the absence of insect pollinators. Selfing species are often the first to recolonise disturbed areas and spread rapidly in the sites to form "weedy" populations (Mulligan and Kevan, 1973). Dipersal mutualisms may play an important role in reaching sites. Plant distributions may be limited by their inability to disperse and subsequently colonise an area. The absence of dispersal mutualisms may thus prevent certain species from re-entering disturbed sites where they may have gone extinct.

The role of mutualisms in determining plant species composition of disturbed communities can, however, not be treated in isolation. The effects of losing a mutualist partner can be compensated for by certain life-form strategies (eg longevity) and, or by reduced dependence on insects for pollination (eg selfing or vegetative propagation) and dispersal.

Bond (1993) adopts a holistic approach to assessing the risk of plant extinctions by incorporating the following biological factors: pollinator and dispersal specificity, breeding systems, life-form strategies and dependence on seeds, into a vulnerability index. This inclusive index provides each species with a hypothetical value between 0 and 1. Plant species which acquire a value close to 1, are postulated to be at a high risk of extinction (vulnerable) in the absence of their mutualistic partners. While those species which obtain a value close to zero are predicted to be at a low risk of extinction. The model predicts that species which are strongly dependant on dispersal and pollinator mutualisms should be at the greatest risk of extinction in the absence of these partners.

Namaqualand was chosen to provide the first empirical test of this mutualism-centred, risk assessment model. The area lies in the semi-arid winter rainfall region of Southern Africa;

where wheat farming is a common source of income to the local inhabitants. Large tracts of natural veld are disturbed by ploughing and then left fallow for a few years. It is in these abandoned wheat fields that mass-flowering occurs: the barren landscape is annually transformed into a kaleidoscope of colour. Although Namaqualand contains approximately 4000 natural plant species (Le Roux and Schelpe, 1988), many of which are endemic, only a small subsample of these natural plants persist in the disturbed areas. These disturbed areas are usually comprised by a few ephemeral or annual species (Le Roux, 1984). Why are these the only plants which are capable of recolonisation. Is an annual life-form a prerequisite for recolonisation of these disturbed areas?

There are numerous advantages of testing this model on the Namaqualand flora. Firstly, the area is characterised by highly synchronised flowering in spring, after sufficient winter rains. This enables all pollination and insect visitation data to be collected simultaneously for a flowering community. Secondly, the flora is comprised by numerous ephemeral and annual species, which flower and set seed over a short time-span thus allowing rapid assessment of reproductive output and breeding systems of these flowering species. Thirdly, a direct comparison can be made between the predicted risk of extinction of each species (according to the model proposed by Bond, 1993) and the actual species composition of disturbed areas. Although Namaqualand is renowned for its spring floral displays; information on the reproductive biology of these flowering species is virtually absent, especially at the community level. Are the majority of these flowering plants selfing or outcrossing and are they dependant on specialist or generalist insects for pollination? Most community studies in Namaqualand have been concerned with flowering phenologies and the role of abiotic and competitive interactions on species distributions (van Rooyen, 1979b; Le Roux et al., 1989). A few studies have investigated insect visitation of these spring flowering species (Struck, 1994). However, nothing is known about the effects of disturbance on plant and pollinator species composition of spring flower communities.

"Before an answer could be given a question itself would have to be discovered" (Boucher, 1985)

This study asks the following key questions:

1) How does plant and animal species composition vary between disturbed and undisturbed areas?

2) Do the following traits differ between disturbed and undisturbed plant communities:
   a) pollinator specificity
   b) breeding systems
   c) life-form strategies(seed dependance)
   d) mode of dipersal

3) Does the vulnerability index proposed by Bond (1993) accurately predict which plant species will be at the greatest risk of going extinct in disturbed areas?

2. DESCRIPTION OF THE REGION

a. Study area

The study was conducted over August and September of 1994 at Skilpad Nature Reserve, which is situated South West of Kamieskroon in central Namaqualand (Fig.1). According to the classification of climatic regions used by the South African Weather Bureau, Namaqualand should be regarded as a desert or poor steppe (Schulze, 1965 cited by van Rooyen, 1979a). The region is characterised by an unpredictable annual rainfall and temperatures which show extensive daily and seasonal fluctuations (van Rooyen et al., 1979a). The area characteristically receives more than 70% of its annual rainfall in winter (Le Roux et al. 1989) and subsequently has a mediterranean type climate. The annual rainfall for Skilpad in 1993 was 380mm, while 1994 showed a marked decline in rainfall (220mm pers. comm. M.Glass). Although the rainfall was relatively low these values are much higher than the average annual rainfall figures for Springbok weather station (162mm pa) (Le Roux et al., 1989). This difference is explained by the strong rainfall gradient from east to west (Struck, pers comm.). This location allows it to receive a considerable amount of coastal fog, which provides essential moisture to the plants in this area. Pollinator activity is frequently inhibited due to unfavourable climatic conditions such as wind, fog, cloud and low temperatures which additionally prevent flowers from opening. The Mean height above sea level is 700m for Skilpad Reserve (pers observation, Fig. 1).

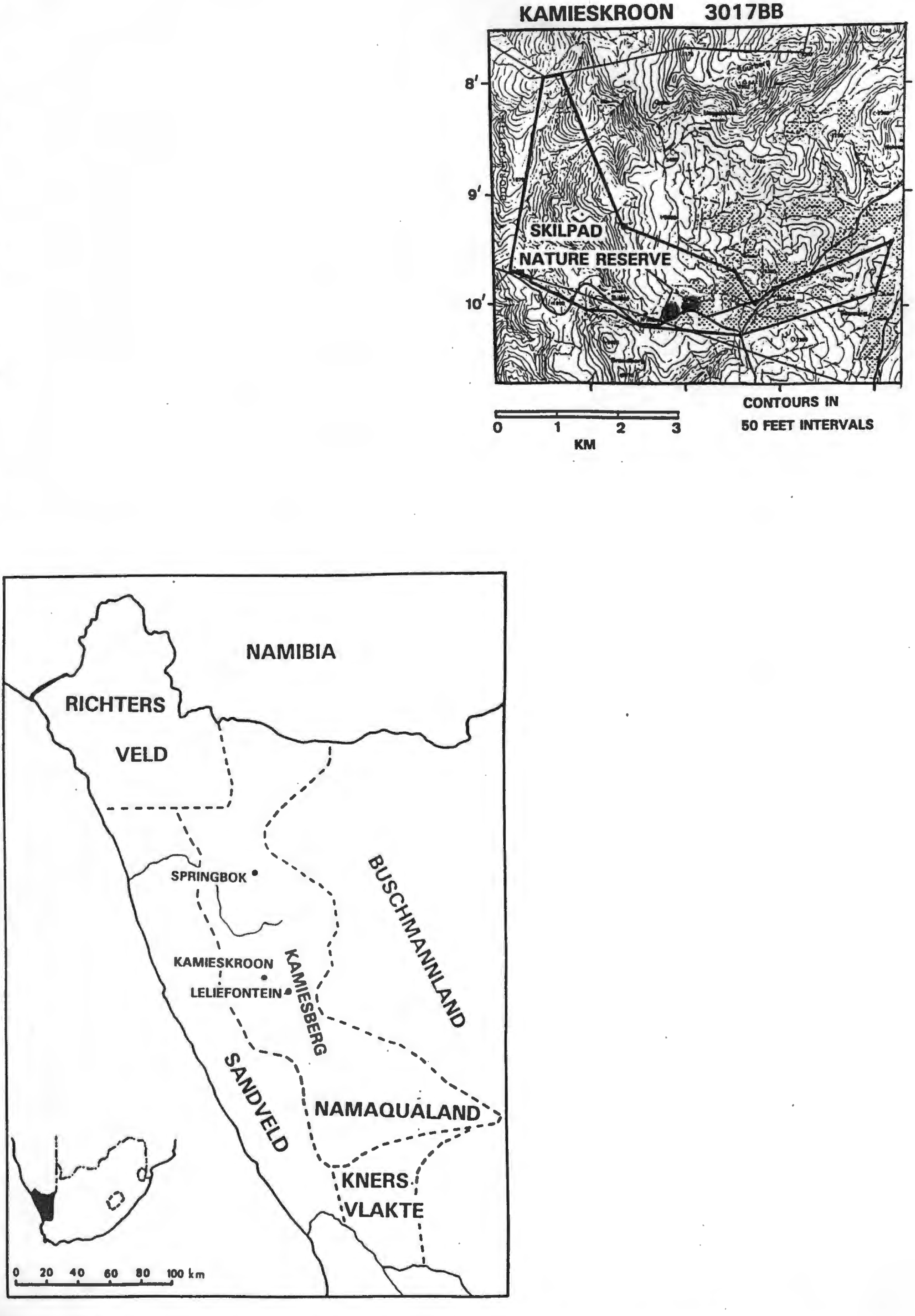

FIG 1. Location of natural and disturbed study sites on Skilpad Nature Reserve in central Namaqualand.

Geologically the area belongs to the Namaqualand Granite-Gneiss Massif (Martin, 1965 as cited by van Rooyen, 1979a) which was formed about 1050 million years ago. The rocks are gneisses, granitic gneisses and granulites. Soils are alluvial, medium to coarse loamy sands, 10-50cm deep on hills and more than 1m in the flats (Le Roux et al., 1989). Weathering of the rocks is predominantly mechanical: the extreme daily temperature fluctuations cause extensive exfoliation. The soil composition of the abandoned fields and the adjacent natural areas are similar. The vegetation is described by Acocks (1975) as Namaqualand Broken Veld, somewhat similar in appearance to Succulent Karroo. The flora is very rich in species, with the vegetation being predominantly dwarf shrubland in which succulents abound. These belong mainly to Mesembryanthemaceae, Euphorbiaceae, Crassulaceae and Asteraceae, but include species from a great number of other families as well (Acocks, 1975; Le Roux, 1984).

b. Study sites

I used a one hectare 'natural'(veld) and 'disturbed'(land) study site on the reserve. I chose areas which were homogenous in terms of topography and soil. The veld site had a slightly North-facing slope while the natural site had a slightly South-facing slope. A hectare was found to include the most common species at each site. A visual survey of Skilpad showed that species composition varied only slightly at different sites on the reserve and repetition of sites was thus considered unnecessary. The specific sites which I chose were less than 200m apart which further decreases the differences between them. The natural site has never been ploughed but has undergone occasional grazing. However, this last occurred three years ago (Glass, pers.comm.). It is important to emphasise that no area is ever entirely undisturbed: the veld study site is grazed by the small mammals and buck which inhabit the nature reserve and this grazing creates a minimal amount of disturbance. This grazing is an ongoing process which is evident as leaf herbivory. The 'disturbed' site is situated on abandoned wheatlands and was last ploughed three years ago, it has undergone no disturbance since then.

c. Floral biology

Inflorescence and partial inflorescence representing the functional unit of visitor attraction or pollination (i.e. blossoms *sensu* Faegri & van der Pijl, 1979) were taken as equivalent to single flowers. Thus the capitula of Asteraceae and the partially separate floral structures of a *Ferraria* were treated as functionally equivalent. The pollinators of some of the geophytes in the area are known: *Lapeirousia silenoides* is known to be pollinated by a long-proposcid fly (Vogel, 1954) with *Pelargonium incrassatum* also being pollinated in this way (Struck, pers comm.). Both species have pink flowers characterised by long, distally narrow straight tubes, with a small orifice at the top which is surrounded by a simple nectar guide (usually a red dot). All these traits are distinctly associated with long-proboscid fly pollination (Johnson, 1992; Whitehead et al., 1987). *P.triste* is visited by a night-active moth (Vogel, 1954). *Gladiolus equitans* possesses a sweet musky scent, and the inflorescence hangs horizontally above the ground with the flowers facing downwards. Both these characteristics suggest that this species may be pollinated by rodents (Rebelo et al. 1987), which are extremely common in the area (Glass, pers comm.). *Ferraria ferrariola* is known to be pollinated by flies (Vogel, 1954, Struck unpublished data).

3. METHODS

Information on breeding systems, pollinator specificity, seed dependence and life-forms was collected and combined into the following vulnerability index proposed by Bond (1993).

$$\mathbf{VI = [BS * PS + DD * DS] * [SD]}$$

Where **VI** is a vulnerability index

BS = breeding system
PS = pollinator specificity
DD = disperser dependence
DS = disperser specificity
SD = seed dependence

The first term in brackets on the right hand side refers to reproductive effects, and the second to demographic effects. Species are ranked for each class using the criteria listed in Table 1

Table 1. Plant attributes and extinction risk. Extinction risk is greatest when the risk of pollinator/ dispersal failure, reproductive dependance on the process and demographic dependance on seeds are all high. PS = pollinator, DS = disperser specificity, BS = breeding system, DD = disperser dependance, SD = population dependance on seeds. Modified from Bond (1993).

Risk of Extinction (Rank)	Risk of process failur (PS,BS)	Dependance on process		Dependance on seeds for survival (SD)
		Pollination (BS)	Dispersal (DS)	
HIGH				
1	single species dependant	Unisexual flowers (Monoecy/ dioecy)	dispersal to specific site critical for survival/recruitment	Short-lived with few seeds
0.8	Pollinated/dispersed by a few closely related specialist vectors	Protandry and obligate outcrossing		Short-lived with many seeds
0.6	pollinated/dispersed by distantly related specialist vectors	Bisexual flowers, facultative selfing		Perrenial with seeds
0.4	Pollinated/dispersed by a set of generalist vectors	Geitonogamy	Requires some sort of dispersal away from parent plant	Long-lived with little/no vegetative propagation
0.2	Pollinated/dispersed by any generalist vectors	Autogamy	Anemochory	some vegetative propagation
0	wind	Apomict/cleistogamy	Achory	Profuse vegetative propagation
LOW				

a. Floral biology and breeding systems

I made detailed observations of the floral biology of the sixteen most common spring flowers in the community, during this study period (Table 2). It is important to emphasise that species composition varies remarkably both spatially and temporally: "not only do the ephemeral populations vary between seasons and localities within a single year, but also from one year to another" (van Rooyen et al. 1979a). The density and composition of the various species can subsequently not be extrapolated to other years. The main question concerning breeding systems was: whether plants can produce seed in the absence of their mutualist pollinators? Pollinator and resource limitation studies were subsequently omitted. The larger species had at least five plants bagged, with nylon mesh bags, to exclude insect pollinators. Only buds were bagged and any open flowers on the plant were excised. Smaller species, which could not support the weight of the bags (especially in the strong winds), were transplanted into an exclosure.

b. Plant densities

The density of each of the sixteen herbaceous flowering species was determined by sampling 5 transects of 25(1m^2) quadrats 2m apart in both the abandoned land and the veld. In each quadrat, the number of blossoms per species was recorded. The relative abundance of each species was then calculated as a percentage of the total number of blossoms per (1m^2) quadrat and determined for the study site (1Ha). Absolute density is a meaningless value in the veld due to the patchy distribution patterns: flowering species were often clumped inbetween shrubs while other sections of the ground were completely devoid of plant cover. The percentage of the veld covered by shrubs was determined by sampling 7 transects of 25 (1m^2) plots, along the natural gradient of the veld, and estimating percentage shrub cover per m^2, this provided an indication of the level of disturbance to this 'natural' stand. A list of the most common shrubs was incorporated as an indication shrub composition in the natural area. Due to the patchy distribution of flowering plants in the lands, density values were divided into dense and sparse patches. Dense patches were identified by the fact that the ground was completely covered by *Ursinia* blossoms, while sparse patches were areas which had visible gaps between *Ursinia* flower heads.

c. Insect visitors

Insect visitor composition and density was determined at both sites. The species composition and density of insects was compared between the sites. These visitation studies were conducted at mid-bloom period in the community (mid-August),between 12h00 and 15h00 hours on three days when the weather was warm, clear and virtually windless (flowers normally only opened between 10h00 and 11h00 depending on the temperature). Insect visitors in the lands and veld was recorded on the same days and as close a time as was possible to those in the veld to prevent bias in timing at which the observations were made. Pollinator specificity for the species which were not observed to be visited was inferred from floral biology. It is important to note that the diversity of spring visitor fauna may fluctuate throughout the season and this data represents a short interval in the duration of the pollinating season.

d. Insect density

In the ploughed land insect abundance and diversity was estimated per m^2 quadrat, this was only carried out in monospecific stands of *Ursinia cakilefolia* since the other species found in the land were extremely sparsely distributed. The number of *Ursinia* per m^2 was recorded as well as the number of *Ursinia* with insect visitors, the percentage of flowers visited per m^2 was then calculated. The number of insects per flower head was also calculated so a total insect value per quadrat could be obtained. Since the distribution of *Ursinia* was distinctly patchy, insect density data were collected for dense and sparse *Ursinia* patches to see whether insect presence was a function of flower density. The data were then pooled together and compared to the data obtained from the natural veld. Insect densities were similarly determined in the natural site except that no distinction was made between flower species, ie quadrats were treated as monospecific stands. This was done so that insect densities between the ploughed land and the natural veld could be made.

The number of *Ursinia* per quadrat was also recorded for the natural site as well as the proportion of these blossoms which were visited so that direct comparisons could be made between the land and veld. Insects were termed visitors if they were actually 'busy' on the blossom, ie an insect remained in contact with the reproductive organs for approximately

30secs. All common visitors were collected and identified to family level. To determine whether flowering species were 'generalist' or 'specialist' pollinated, observations of insect visitors were attempted for all species occurring in the veld. Since the lands contained a subsample of the flowering community found in the veld, pollinator specificity studies were only conducted in the veld. Pollinator specificity was estimated by walking around in the natural area and checking for the presence of insect visitors, on at least 50 randomly chosen individuals of each species.

e. Breeding systems (Fruit set)

The ability to set seed spontaneously was quantified by determining the percentage of flowers on a plant which form fruit when pollinators are excluded. For the Asteraceae, most species had a single blossom per plant, however, *Arcotheca calendula, Osteospermum hyoseroides* and *Gorteria diffusa* had numerous blossoms per plant. The geophytes all had a number of blossoms constituting an inflorescence on the plant. *Gorteria* is additionally unusual in that each inflorescence only develops a single fruit. These fruit set values were compared with open (control) plants which were unmanipulated and were permitted to set seed naturally. In all multiple seeded fruits the number of seeds per fruit was determined. The Asteraceae species form a calypsa (single seeded fruit formed from a solitary carpel). Since only some of the flowers on an Asteraceae cpitulum are fertile, fruit set was only determined for these fertile florets. Disperser specificity and disperser dependence was determined from the structure of the fruits (ie winged fruits indicate wind dispersal), this information was tabulated (Table 3)

f. Seed Dependence (Vegetative propagation)

The capacity to propagate vegetatively was determined by investigating the underground structures of all the geophytes. Five bulbs or corms were measured for each species. Size (volume) was taken as a surrogate measure of the lifespan of the species. The number of bulblets or cormlets was also recorded to determine the ability to reproduce vegetatively. This information was tabulated and represented graphically.

g. Statistical analyses

Mann Whitney tests for non-parametric data were conducted on the insect and fruit set data to determine whether statistically significant differences occur between sites and treatments respectively.

4. RESULTS

The natural site had a greater diversity of plants than the disturbed site (Table 2). Only six of the sixteen flowering species from the natural plant community were present in the abandoned lands, five of them annuals and four belonging to the Asteraceae. All of these species except *Dimorphotheca sinuata* were also present in the veld. Asteraceae is the dominant family in the natural site with seven species. There is a distinct dichotomy in the life-form strategies in the veld: over half the species were annuals and the remainder geophytes (Table 3). The geophytes mainly consist of corms except for *Oxalis* which is bulbous (Appendix 2) and all except *Babiana curviscapa* and *Oxalis* have complex flowers (Table 3). The annuals all have characteristically simple flowers or capitula in the case of Asteraceae. Bright coloured flowers predominated in this area: orange, yellow and bright pink were the dominant colours. The disc and ray florets comprising capitula differ in their sexual systems: the ray florets are usually sterile or female while the disc florets are bisexual. All other species had bisexual flowers and all of the geophytes were protandrous.

The transition from the natural to the disturbed site was accompanied not only by a reduction in species abundance but also by changes in the density of the constituent species (Fig.2 & Fig.3a). *Osteospermum hyoseroides* and *Ursinia cakilefolia* were the most abundant species in the natural veld and both occured in similar densities (Fig.2). *Gorteria, Lapeirousia* and *Dorotheanthus* were also quite common in the veld. The remaining species were relatively scarce. In comparison, *Ursinia* entirely dominated the abandoned lands (72.19% Fig 3b), and the other species only featured in the sparse patches. The complete absence of *Osteospermum hyoseroides* at the disturbed site was suprising. *Ursinia* density exceeds 95% in the dense patches (Fig 3b). *Cotula* and *Arctotheca* occured in greater densities in the land than in the veld and were relatively common at this site (Fig 2, 3a & 3b). The natural veld site has 50% of the area covered in shrubby plants (Appendix) in comparison to the land which only had no additional form of vegetation cover besides the flowering herbs.

Table 2. Spring floral composition of the natural and disturbed study sites at Skilpad Nature Reserve.

Natural site

ASTERACEAE
Arctotheca calendula (L.) Levyns.
Arctotis fastuosa (L.) Jacq.
Cotula barbata (L.) DC.
Gorteria difussa ssp diffusa (L.) Thunb.
Osteospermum hyoseroides (L.)(DC.) T. Norl.
Ursinia cakilefolia (DC.)

BRASSIACEAE
Heliophila variabilis (L.) Burch. ex DC.

GERANIACEAE
Pelargonium incrassatum (Andr.) Sims
Pelargonium triste (L.)L'Hent

IRIDACEAE
Babiana curviscapa G.J. Lewis
Ferraria ferrariola (Jacq.) Willd
Gladiolus equitans Thunb.
Lapeirousia silenoides (Jacq.) Ker-Grawl

MESEMBRYANTHEMACEAE
Dorotheanthus bellidiformis ssp. hestermalensis (Burm. F.) N.E. BR. Ilenf. & Struck

OXALIDACEAE
Oxalis sp

Disturbed site

Arctotheca calendula
Cotula barbata
Dimorphotheca sinuata
Ursinia cakilefolia
Heliophila variabilis
Oxalis sp.

Table 3. Summary of floral biology characteristics for the 16 most common spring flowers growing at the natural site.

SPECIES	COLOUR	SIMPLE/ COMPLEX FLOWERS	SEXUAL SYSTEM: STRUCTUR OF CAPITULA/FLOWERS	LIFE FORM	PRESENT IN LAND/VELD/BOTH
ASTERACEAE					
A.calendula	Yellow	simple	Ray florets sterile Disc florets bisexual	Annual	B
A.fastuosa	Orange	simple	Ray florets female Disc florets bisexual	Annual	V
C.barbata	Yellow	simple	Ray florets absent Marginal florets female Central florets bisexual	Annual	B
D.sinuata	Orange	simple	Ray florets female/sterile Disc florets bisexual/male	Annual	L
G.diffusa ssp.diffusa	Orange + green,black & white markings	simple	Ray florets sterile Disc florets bisexual	Annual	V
O.hyoseroides	Yellow	simple	Ray florets female Disc florets sterile/male	Annual	V
U.cakilefolia	Orange	simple	Ray florets neuter Disc florets bisexual	Annual	B
BRASSIACEAE					
H.variabilis	White	simple	bisexual	Annual	B
GERANIACEAE					
P.incrassatum	Pink	complex	Bisexual, protandrous	Geophyte	V
P.triste	Creamy yellow	complex	Bisexual, protandrous	Geophyte	V
IRIDACEAE					
B.curviscapa	Purple	complex	Bisexual, slight protandry	Geophyte	V
F.ferrariola	Pale blue-green	complex	Bisexual, protandrous	Geophyte	V
G.equitans	Brick red with lower perianth lobes Yellow-green & red tips	complex	Bisexual, protandrous	Geophyte	V
L.silenoides	Pink + cream markings & white perianth tube	complex	Bisexual	Geophyte	V
MESEMBRYANTHEMACEAE					
D.bellidiformis ssp.hestermalensis	Pink-white	simple	Bisexual, protandrous	Annual	V
OXALIDACEAE					
Oxalis sp.1	Yellow	simple	Bisexual, tristylous	Geophyte	B

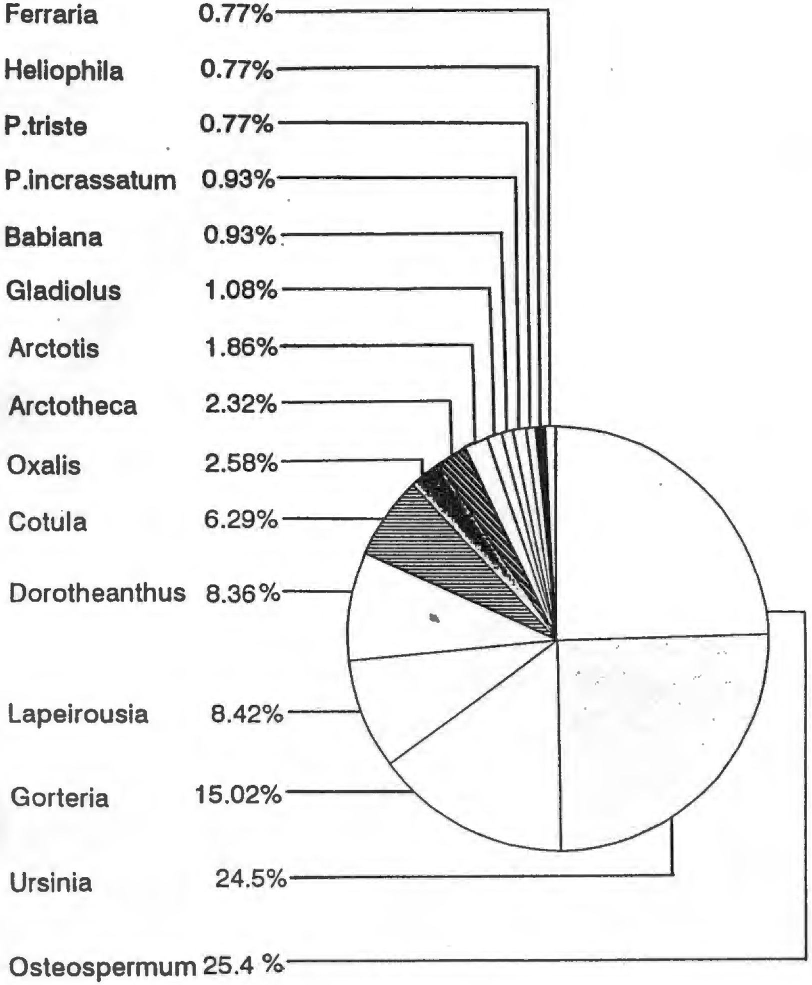

FIG 2. Relative densities of the most common spring flowering species growing at the natural study site.

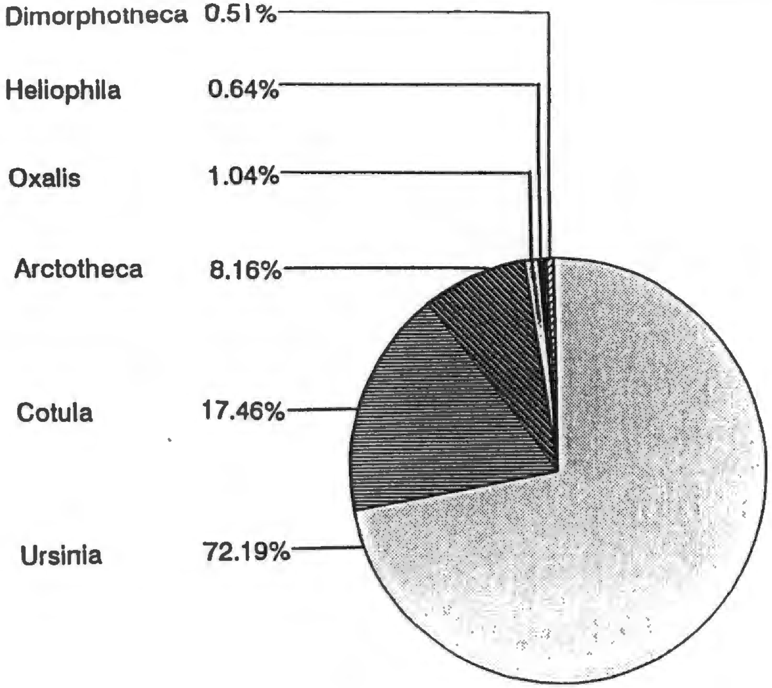

FIG 3a. Relative densities of spring flowering species growing in the abandoned lands.

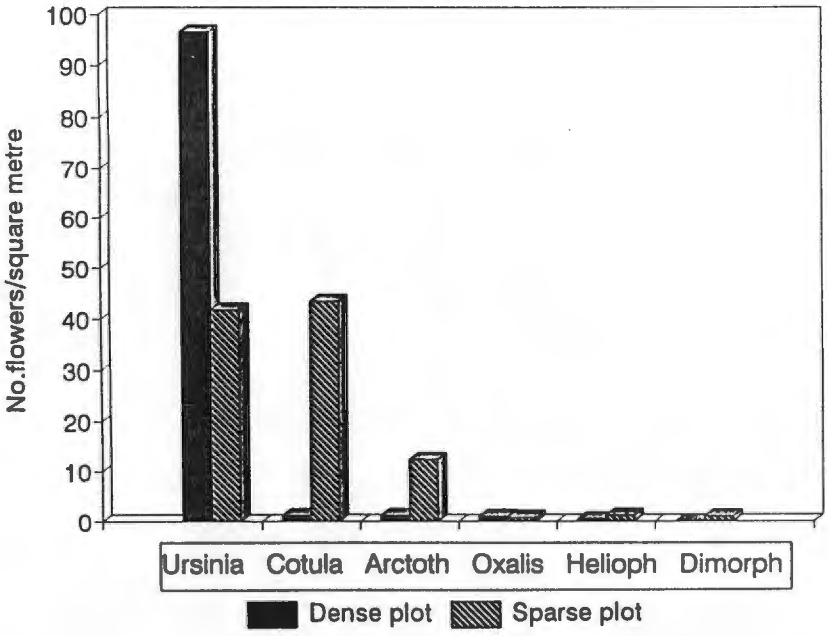

FIG 3b. Floral densities in the abandoned lands, demonstrating compositional differences between dense and sparse *Ursinia* patches.

a. Insect visitors

The patchiness of *Ursinia* in the abandoned lands, is evident in the fact that there are on average over 300 heads per quadrat in the dense patches compared to less than 50 heads per quadrat in the sparse patches (Fig 4A), this difference was obviously highly significant ($p < 0.001$, $N = 28$). The percentage of flowers visited per quadrat did not differ significantly between dense and sparse *Ursinia* patches (Fig 4B, $p > 0.05$, $N = 28$). The total insect count for the sparse patches was greater than in the dense patches (Fig 5A), but not significantly so ($p > 0.05$, $N = 26$). Over 95% of the insect visitors observed in both the dense and the sparse *Ursinia* patches consisted of Tenebrionoidae (Fig 5B); these small black beetles are less than 2mm long and had no hairs on them for carrying pollen.

The dense and sparse data from the land were pooled together and compared to the data obtained from the veld. There were far more *Ursinia* heads per m^2 in the land than in the veld (Fig 6A), the difference was found to be statistically significant ($p < 0.0001$, $N = 37$). A similar proportion of flowers is visited at both the land and the veld site (Fig 6B). There was no significant difference in number of insects encountered on *Ursinia* heads between the two sites (Fig 7A).
Although Tenebrionoids were entirely absent from the natural study site (Fig 7B).

Total flower density per m^2 was significantly higher in the land than in the veld (Fig 8A, p , 0.001, $N = 41$). A significantly higher percent of flowers were visited in the land than in the veld (Fig 8B, $p < 0.05$, $N = 41$). The number of insects per m^2 is far higher in the land than in the veld when all flowers are considered (Fig 9A, $p < 0.0001$, $N = 41$). However, this insect abundance in the abandoned lands was comprised almost entirely by Tenebrionoidae beetles (Fig 9B), and these beetles are virtually absent from the veld, even when all flower visitors per m^2 are recorded.

b. Insect specificity

In the natural veld, *Arctotis fastuosa, Osteospermum hyoseroides* and *Ursinia cakilefolia* were all visited by a set of generalist insects; which included Hopliinids (monkey beetles), Melyrids, bee-flies (Bombylidae) and some hemipterans (Table 4). A considerable degree of

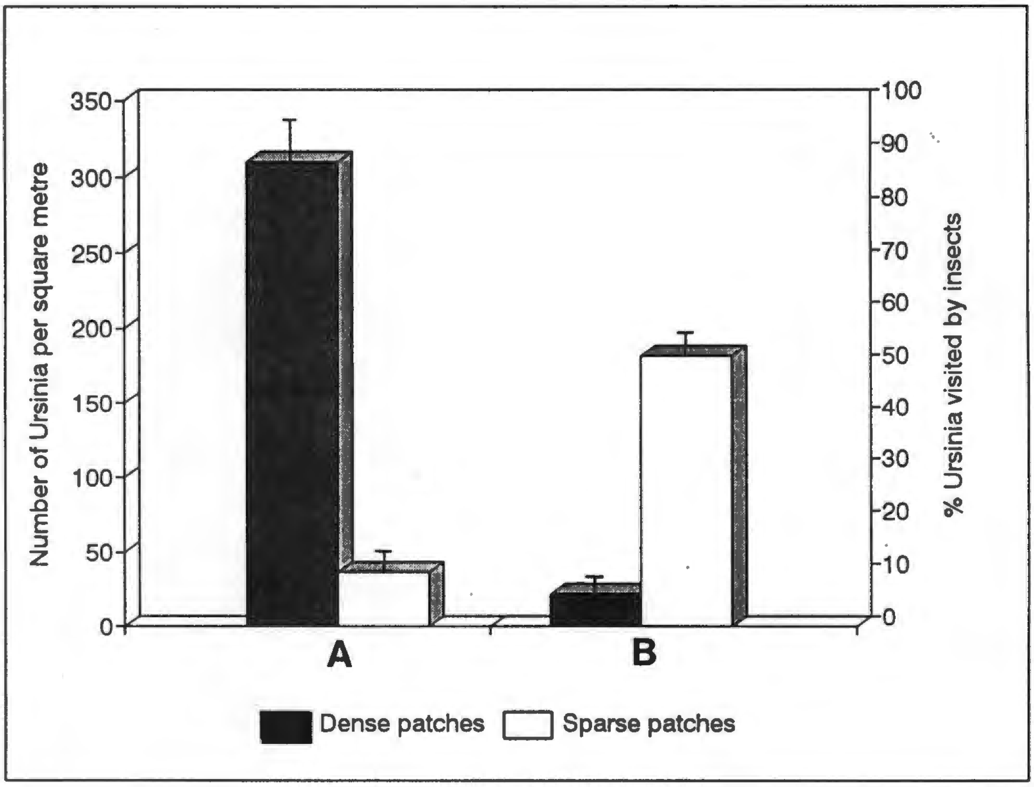

FIG 4. A - *Ursinia* densities in sparse and dense patches at the disturbed site. B - The percentage of *Ursinia* heads in dense and sparse patches which were visited by insects. Bars = 1 Standard Error.

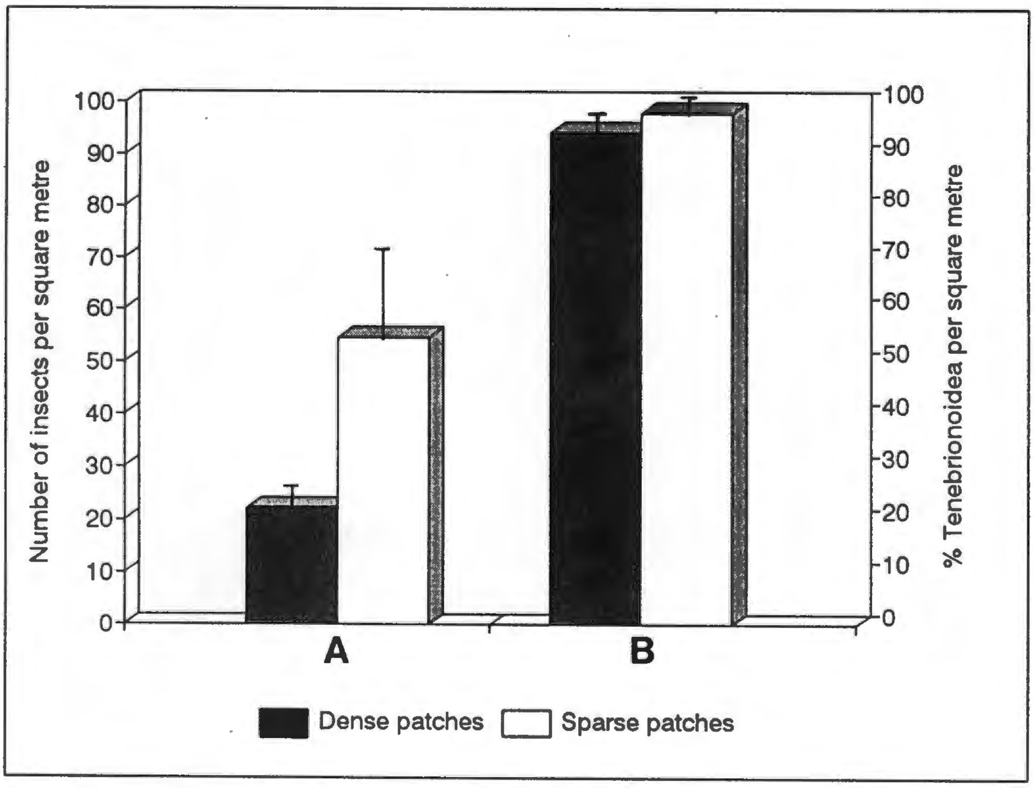

FIG 5. A - The total number of insects per quadrat for dense and sparse patches at the disturbed site. B - The percentage of insect visitors to *Ursinia* comprised by Tenebrionid beetles. Bars = 1 Standard Error.

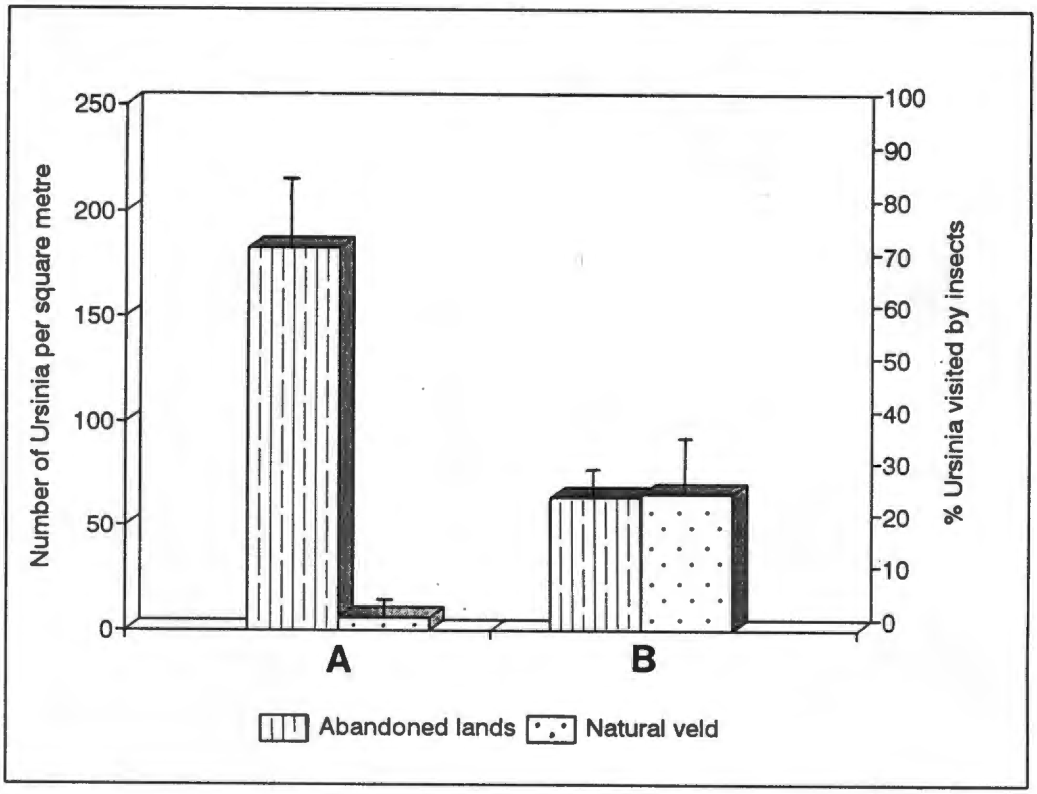

Fig 6. A - *Ursinia* densities in the land (data from sparse and dense patches pooled), and veld. B - The percentage of *Ursinia* heads per quadrat, which were visited by insects in the land and veld. Bars = 1 Standard Error.

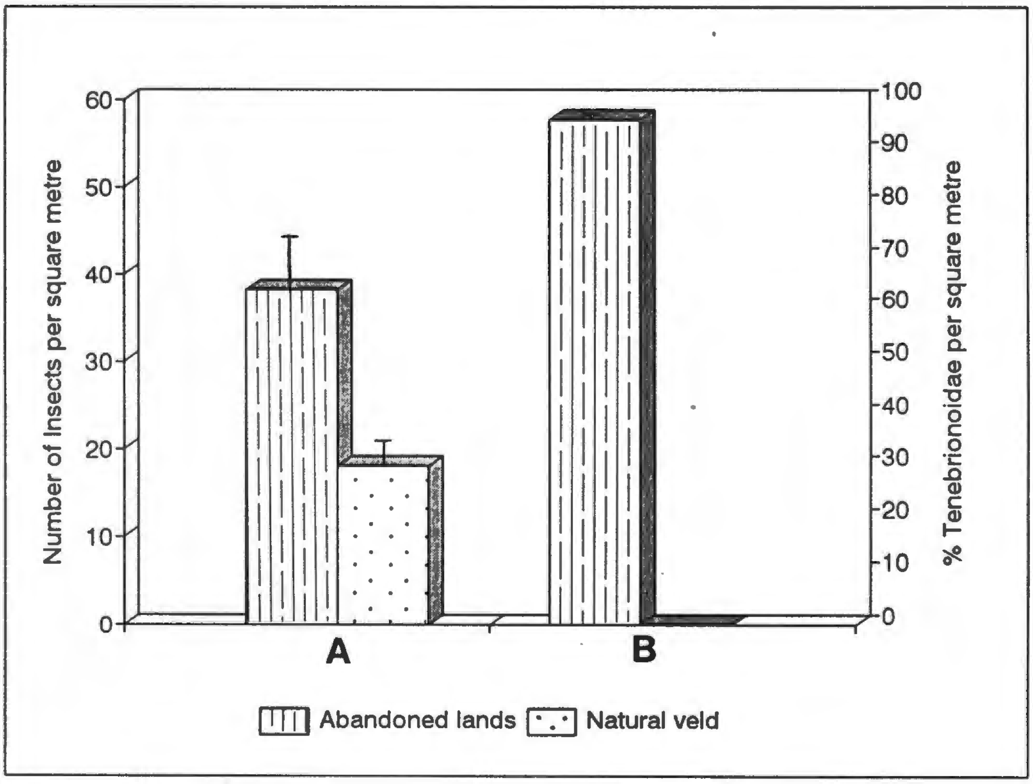

FIG 7. A - Number of insect visitors per quadrat in the land (data for dense and sparse patches pooled) and veld. B - The percentage of insects per quadrat comprised by Tenebrionid beetles. Bars = Standard Error.

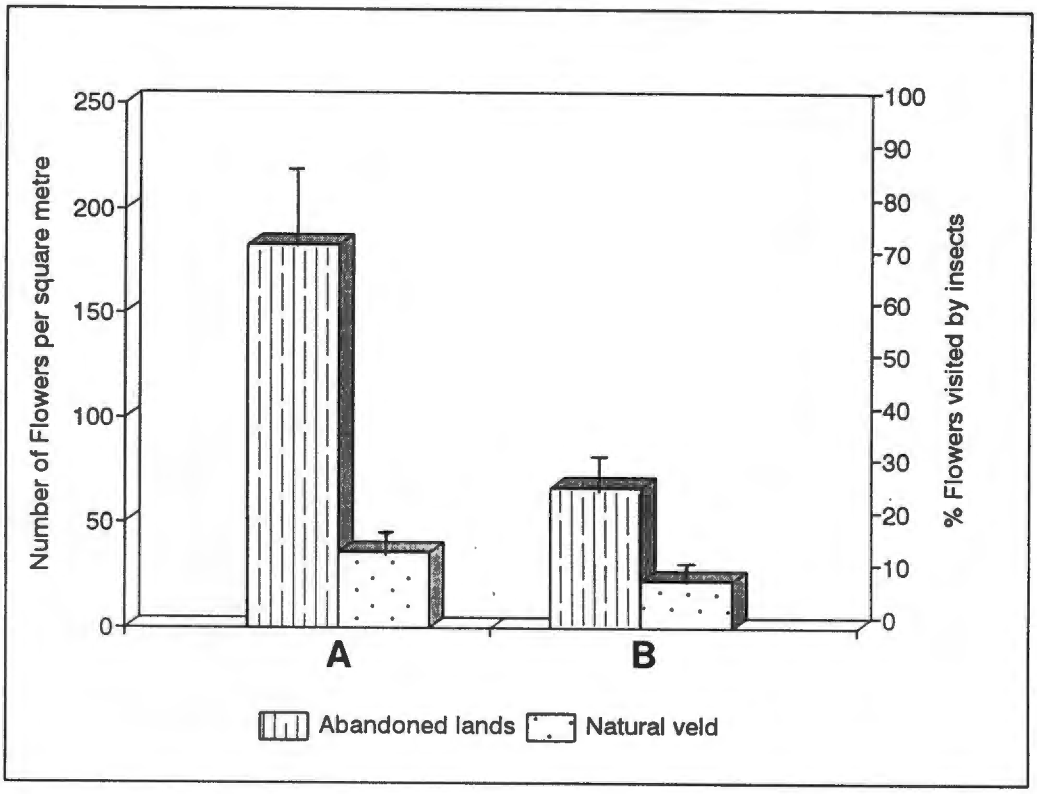

FIG 8. A - Total number of flowers per quadrat in the land and veld. B - Percentage of flowers per quadrat in the land and veld which were visited by insects. Bars = Standard Errors.

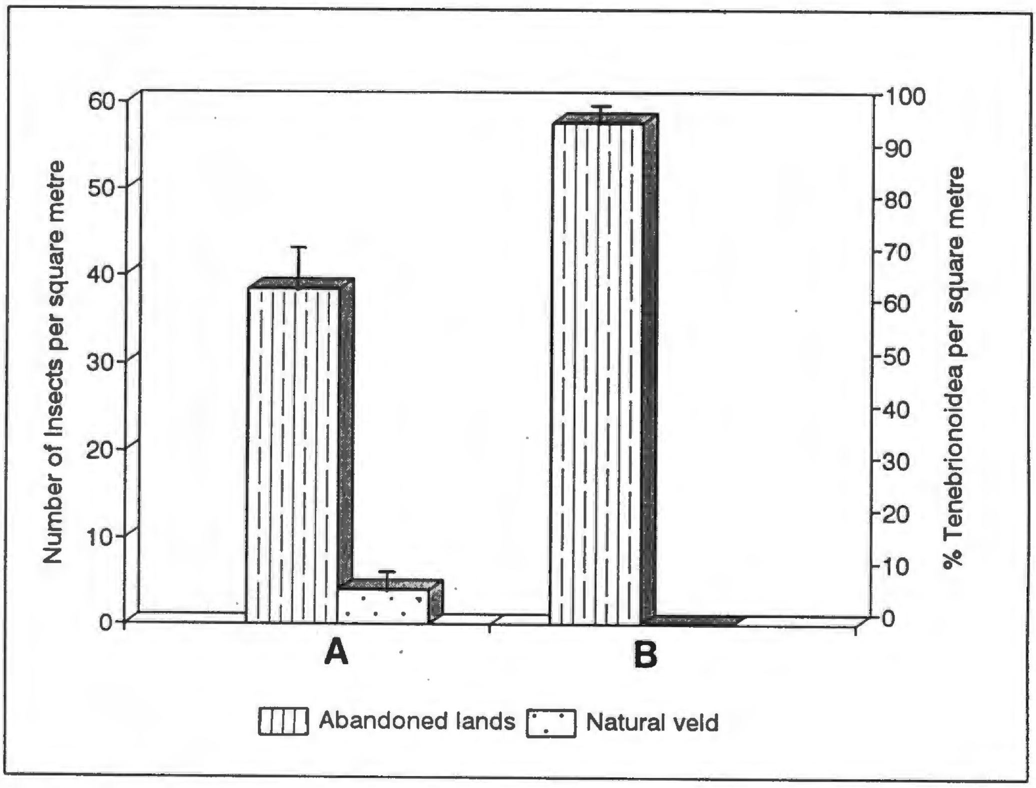

FIG 9. A - Number of insect visitors per quadrat in the land and veld. B - Percentage of insect visitors in the land and veld comprised by tenebrionid beetles. Bars = 1 Standard Error.

Table 4. Insect visitors to spring flowering species growing at the natural site. This provides an indication of the degree of pollinator specificity.

	Floral Host							
Insect Visitor	ARCTOT	ARCTO	COT	GORT	OSTE	URS	HELIO	DOROT
Coleoptera								
Scarabaeidae								
Rutelinae								
Hopliinae		19			24	9		
Melyridae		21			22	18		11
Hemiptera								
Heteroptera								
Lygaedae	1							1
yellow spot	1	2		3	2	1		3
Diptera								
Bombylidae								
bee-fly		2	3	23	41	2		
long-tongued fly		1		1		1		
Hymenoptera								
ant	5	5	5	3	1	1	3	

No visitors were observed for B.curviscapa, L.silenoides, G.equitans
Oxalis sp, P.triste and P.incrassatum

visitor sharing occurs between these species. These flowering species should therefor be more tolerant of a change in insect assemblage. Both *Gorteria diffusa* and *Osteospermum hyoseroides* received numerous visits by bee-flies (Bombylidae) (Table 4). *Gorteria* was not observed to receive any visits from beetles. Seven of these flowering species had ants observed visiting their flowers. *Dorotheanthus, Heliophila* and *Arctotis* received hardly any insect visitors (Table 4). The geophytes in the natural area are all pollinated by specific insects which are adapted to removing nectar from the complex flowers, many of which have long perianth tubes. *Ferraria ferrariola* is an exception amongst the geophytes since it is pollinated by flies. The specialist pollinator guilds of the geophytes were apparently absent from the natural site. The most abundant floral visitors in the natural veld were Coleopteran: Hopliinae and Melyridae, and Bombylidae (bee flies)(Table 4). Hemipterans and ants (Hymenoptera) were also quite common flower visitors.

c. Breeding systems

Five species from the natural plant community were autogamous: *Arctotheca calendula, Cotula barbata, Ursinia cakilefolia, Heliophila variabilis* and *Dorotheanthus bellidiformis* all set seed spontaneously in the absence of insect pollinators (Table 4). All of these autogamous species, except *Ursinia*, do not differ significantly (according to Mann-Whitney test) in % fruit set between the open and transplanted plants. The enclosed *Ursinia*, however, had a significantly lower seed set than the open plants, these flowers also remained open for much longer than the natural flowers. *Gorteria* and *Arctotheca* flowers were self-incompatible and were found to set seed when pollen was moved around amongst flowers in the capitulum (geitonogamy). *Gorteria* is the only Asteraceae species which has a high natural fruit set (c.a. 96%, Table 4). In *Arctotis fastuosa* only the outer 2-3 whorls of disc florets develop seed although most florets develop feathery structures at their bases, these are usually empty. *Ursinia cakilefolia* similarly only develops fruit in the outer 2/3 whorls of flowers. In contrast, *Dimorphotheca sinuata* formed fruit in all except the inner one or two whorls of the inflorescence. *Osteospermum* and *Dimorphotheca* have relatively high fruit set values. None of the geophytes set fruit in the absence of pollinators indicating self-incompatibility. They all have extremely low natural fruit set values ranging from 8.5% in *Babiana* to 65.5% in *Gladiolus* (see Table 4) .

Table 5. Breeding systems of spring flowering species growing at the natural site. The ability to set fruit in the absence of insects indicated either autogamy or geitonogamy. Failure to set seed in the absence of insect visitors indicates self-incompatability. The differences between natural and enclosed fruit set was investigated for each species by Mann-Whitney test. ** indicates significant differences at the 0.05 level. *** indicates significant differences at the 0.001 level. NS = Not significant difference.

PLANT SPECIES	TEST	PLANT (N)	TOTAL # OF FLOWERS	TOTAL # OF FRUIT	% FRUIT SET	AUTO-/GEITONOGAMY /NEITHER	Z
ASTERACEAE							
Arctotheca calendula	open	7	276	150	54.35	A	0.3320
	enclosed	5	185	109	58.92		NS
Arctotis fastuosa	open	7	2320	457	19.7	G	0.0021
	bagged	5	1776	0	0		**
Cotula barbata	open	6	345	55	15.94	A	0.1390
	enclosed	9	201	43	21.39		NS
Dimorphotheca sinuata	open	8	950	750	78.95		
	enclosed	10	!			/	
Gorteria diffusa ssp. diffusa	open	9	140	134	95.71	G	0.0008
	bagged	6	54	0	0		***
Osteospermum hyoseroides	open	6	288	212	73.61	A	0.0025
	enclosed	6	288	0	0		**
Ursinia cakilefolia	open	7	1110	405	36.49	A	0.0027
	enclosed	5	870	50	5.75		**
BRASSIACEAE							
Heliophila variabilis	open	10	204	204	100	A	0.3173
	enclosed	10	160	160	100		NS
GERANIACEAE							
Pelargonium incrassatum	open	6	380	66	17.37	/	0.0055
	bagged	5	232	0	0		**
Pelargonium triste	open	6	51	8	15.69	/	0.0169
	bagged	5	31	0	0		**
IRIDACEAE							
Babiana curviscapa	open	7	82	7	8.54	/	0.00056
	bagged	7	121	0	0		**
Ferraria ferrariola	open	6	63	25	39.68	/	0.00379
	bagged	5	54	0	0		**
Gladiolus equitans	open	7	29	19	65.52	/	0.0004
	bagged	8	32	0	0		***
Lapeirousia silenoides	open	7	135	25	18.52	/	0.00207
	bagged	6	110	0	0		**
MESEMBRYANTHEMACEAE							
Dorotheanthus bellidiformis ssp. hestermalensis	open	18	32	32	100	A	0.3179
	enclosed	12	15	15	100		NS

* Oxalis species were assumed not to set seed without insects

! Plants died after transplanting

d. Dispersal

Wind dispersal is common in this spring flowering community: all species except *Gorteria, Babiana* and *Ferrarria* have fruits which are structurally adapted for wind dispersal (Table 6). The capsule of *Dorotheanthus bellidiformis* opens to release the seeds when it gets wet. The Asteraceae species all have cypselas (single seed per carpel and each flower has only one carpel), except for *Gorteria* which has more than one seed per fruit (X = 2.1, N = 36, SD = 0.8). However, as already mentioned *Gorteria* forms a fruit from the whole capitulum (blossom) as opposed to each flower, thus the level at which fruit forms is different and not directly comparable. The remaining species all have multiple seeded fruits. The fruit of the two *Pelargonium* species is termed a schizocarp and consists of the elongated style which splits into 5 mericarps, each carrying one seed in its base. Each mericarp has a long slender tail which curls up when fully ripe but uncurls and straightens when it is moistened, on drying it again curls up, having a corkscrew like action to the sharp pointed base.

e. Vegetative propagation

Only three of the six geophytes displayed any capacity for vegetative propagation (Appendix 2). The *Oxalis* species produced numerous tiny bulblets along the length of its underground stem. *Ferraria ferrariola* produces a new corm annually, which grows onto of last years corm, so that eventually a string of different sized corms is obtained. *Gladiolus equitans* does not produce many cormlets, it sometimes splits into two bulbs when it develops a new leaf and the new, smaller bulb, is nested in the larger one. *L.silenoides, B.curviscapa, P.incrassatum* and *P.triste* do not reproduce vegetatively. *P.triste*, however, has an enormous underground horizontal corm implying a relatively long life-span. Since all of these geophytic species have extremely low natural fruit set (Table 5) vegetative reproduction would be expected to be an important form of reproduction in the absence of insect pollinators. When Lifespan is plotted against ability to propagate vegetatively three geophytic species were found to be at risk of going extinct in the absence of pollinators. These were *Babiana, Lapeirousia* and *Pelargonium incrassatum*. All have a low natural fruit set (Table 5) and displayed no ability to propagate vegetatively (Fig 10). *Pelargonium triste*, which is relatively long-lived and *Oxalis* and *Ferraria*, which are capable of considerable vegetative propagation, are all at a low risk of going extinct in the absence of insect pollinators.

Table 6. Summary of diaspore structure and modes of dispersal exhibited by the natural spring flowering community.

PLANT SPECIES	DIASPORE STRUCTURE	DISPERSAL VECTOR	SEEDS/ FRUIT	N	SD
ASTERACEAE Arctotheca calendula	Diaspore with hairy pappus	wind	1*		
Arctotis fastuosa	Diaspore with hairy pappus	wind	1*	36	0
Cotula barbata	Tiny winged dispores	wind	1*		
Dimorphotheca sinuata	Winged and tubular diaspores	Winged diaspores = w tubular diaspores = fal	1*		
Gorteria diffusa ssp. diffusa	Synaptospermous	animal (small mammal	2.1	40	0.8
Osteospermum hyoseroides	Winged diaspores	wind	1*		
Urcinia cakilefolia	Diaspores has pappus of five conspicuous white scales.	wind	1*		
BRASSIACEAE Heliophila variabilis	Dehiscent pod	wind	17.35	43	2.69
GERANIACEAE Pelargonium incrassatum	Each diaspore has a long mericarp which is feathered and has an anchoring device	wind	5	6	0
Pelargonium triste	Each diaspore has a long mericarp which is feathered	wind	5	4	0
IRIDACEAE Babiana curviscapa	Xerochastic	animal/bird	!		
Ferraria ferrariola	Xerochastic	animal/bird	16.25	12	8.6
Gladiolus equitans	Xerochastic	wind	56	6	9.79
Lapeirousia silenoides	Xerochastic	!	!		
MESEMBRYANTHEMACEAE Dorotheanthus bellidiformis ssp. hestermalensis	Hydrochastic	ombrohydrochorous	18	8	5.4

* Cypsela: single seed per carpel and fruit consists of only one carpel.
! Unknown

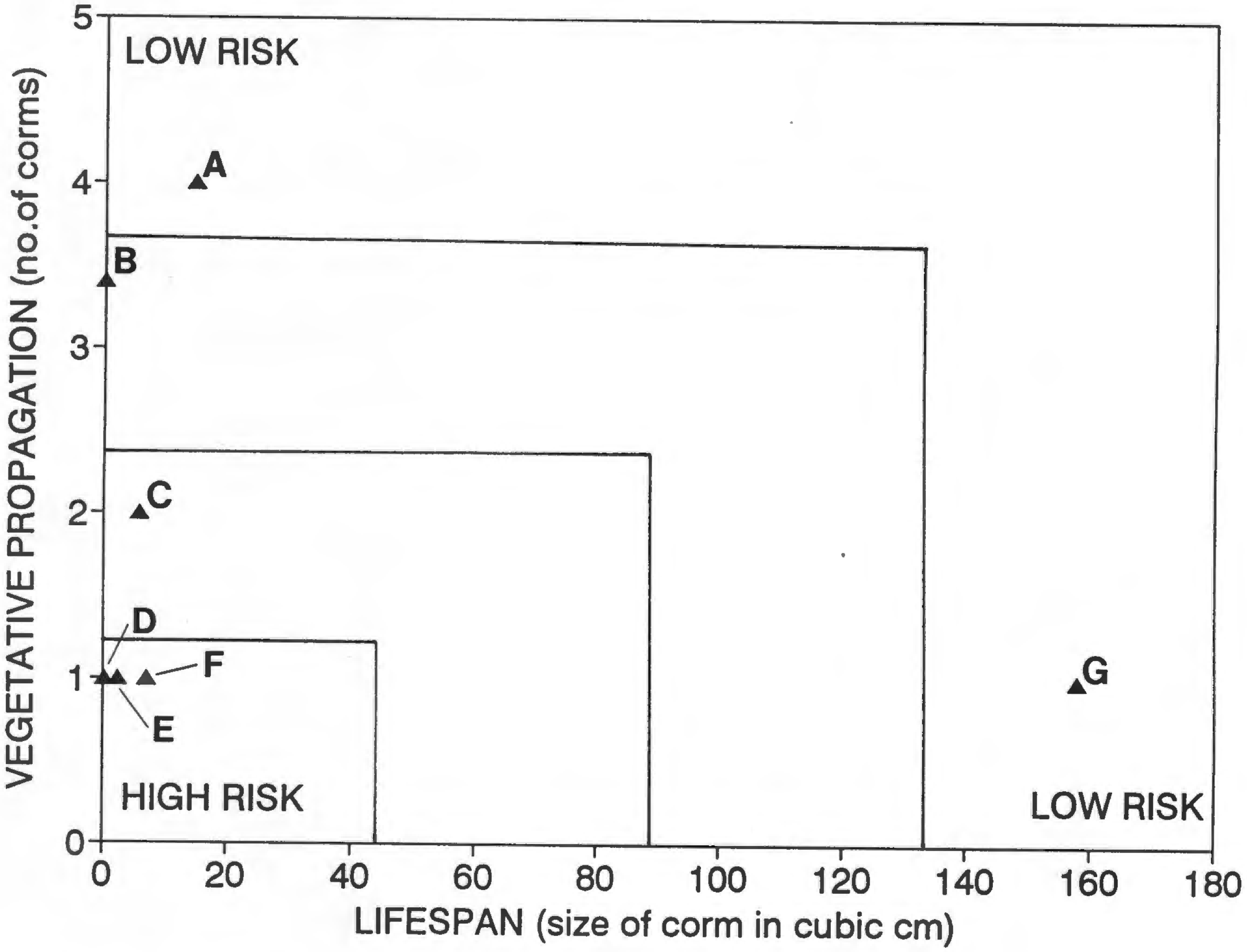

FIG 10. **Plot of geophyte lifespan against degree of vegetative propogation indicating risk of plant extinction in the absence of insect pollinators. A =** ***Ferraria ferrariola*** **B =** ***Oxalis sp*** **C =** ***Gladiolus equitans*** **D =** ***Lapeirousia silenoides*** **E =** ***Pelargonium incrassatum*** **F =** ***Babiana curviscapa*** **G =** ***Pelargonium triste*****.**

Gladiolus equitans, which is capable of limited vegetative propagation is inbetween the low and high risk area.

f. Vulnerability Indices

Table 7 summarises the values for each term in the vulnerability index. These values are subjective and should be viewed as a relative indication of vulnerability (Table 1). All autogamous species have low breeding system values since they are not dependant on insects for successful pollination. Geitonogamous species are dependant on insects but not outcrossing for seed set. The self-incompatible species, mainly the geophytes, are ranked between 0.6 and 0.8 depending on whether they are protandrous or not. Pollinator specificity was low for the annuals most of which were visited by a variety of insects (Table 4). The geophytes are all dependant on more specialised insect pollinators especially *L.silenoides* and *P.incrassatum* which both have long narrow perianth tubes. Only species with fleshy fruits or seeds are dependant on mutualisms for dispersal. The majority of these species have seeds adapted for wind dispersal and subsequently have low disperser dependence (DD) and disperser specificity (DS) values. Seed Dependence is high for the annuals and intermediate for the geophytes.

A plot of pollinator limited seed set (BS*PS) against Seed Dependence (SD) illustrated that *Oxalis* has the lowest risk of going extinct. *Arctotheca, Cotula, Dimorphotheca, Dorotheanthus, Heliophila, Ursinia, Osteospermum, Arctotis, Gorteria, Ferraria* and *Gladiolus* were all found in the low risk area. *Pelargonium triste* is at an intermediate risk of going extinct in the absence of insect pollinators. *Babiana, Lapeirousia* and *Pelargonium incrassatum* are at the greatest risk of going extinct in this area (Fig 11, Table 7).
The Iridaceae and *Pelargonium* species seem to be the most extinction prone while the Asteraceae are much less prone to extinction. This model thus predicts that only a few geophytic species should suffer from local extinction in the disturbed areas due to the absence of mutualist partners.

5. DISCUSSION

Namaqualand is characterised by large tracts of ploughed lands, interspersed between fragments of natural vegetation, Skilpad Nature Reserve is no different from this land-use

Table 7. Ranks obtained for the terms comprising the vulnerability index. BS = breeding system, PS = pollinator specificity, DD = disperser dependance, DS = disperser specificity, SD = seed dependance, VI = vulnerability index VI = [BS*PS + DD*DS] *SD. Refer to Table 1 for explanations of the ranking procedure.

SPECIES	BS	PS	DD	DS	SD	VI
ASTERACEAE						
A.calendula	0.1	0.2	0	0	0.8	0.016
A.fastuosa	0.4	0.2	0	0	0.8	0.064
C.barbata	0.1	0.2	0	0	0.8	0.016
D.sinuata	0.1	0.2	0	0	0.8	0.016
G.diffusa ssp.diffusa	0.4	0.2	0.4	0.4	0.9	0.216
O.hyoseroides	0.9	0.2	0	0	0.8	0.144
U.cakilefolia	0.1	0.2	0	0	0.8	0.016
BRASSIACEAE						
H.variabilis	0.1	0.2	0	0	0.8	0.016
GERANIACEAE						
P.incrassatum	0.8	1	0	0	0.4	0.32
P.triste	0.8	0.8	0	0	0.2	0.128
IRIDACEAE						
B.curviscapa	0.8	0.6	0.4	0.4	0.4	0.256
F.ferrariola	0.8	0.6	0.4	0.4	0.1	0.064
G.equitans	0.8	0.6	0.4	0	0.1	0.048
L.silenoides	0.8	1	0	0	0.4	0.32
MESEMBRYANTHEMACEAE						
D.bellidiformis ssp.hestermalensis	0.1	0.2	0	0	0.8	0.016
OXALIDACEAE						
Oxalis sp1.	0.8		0	0	0	0

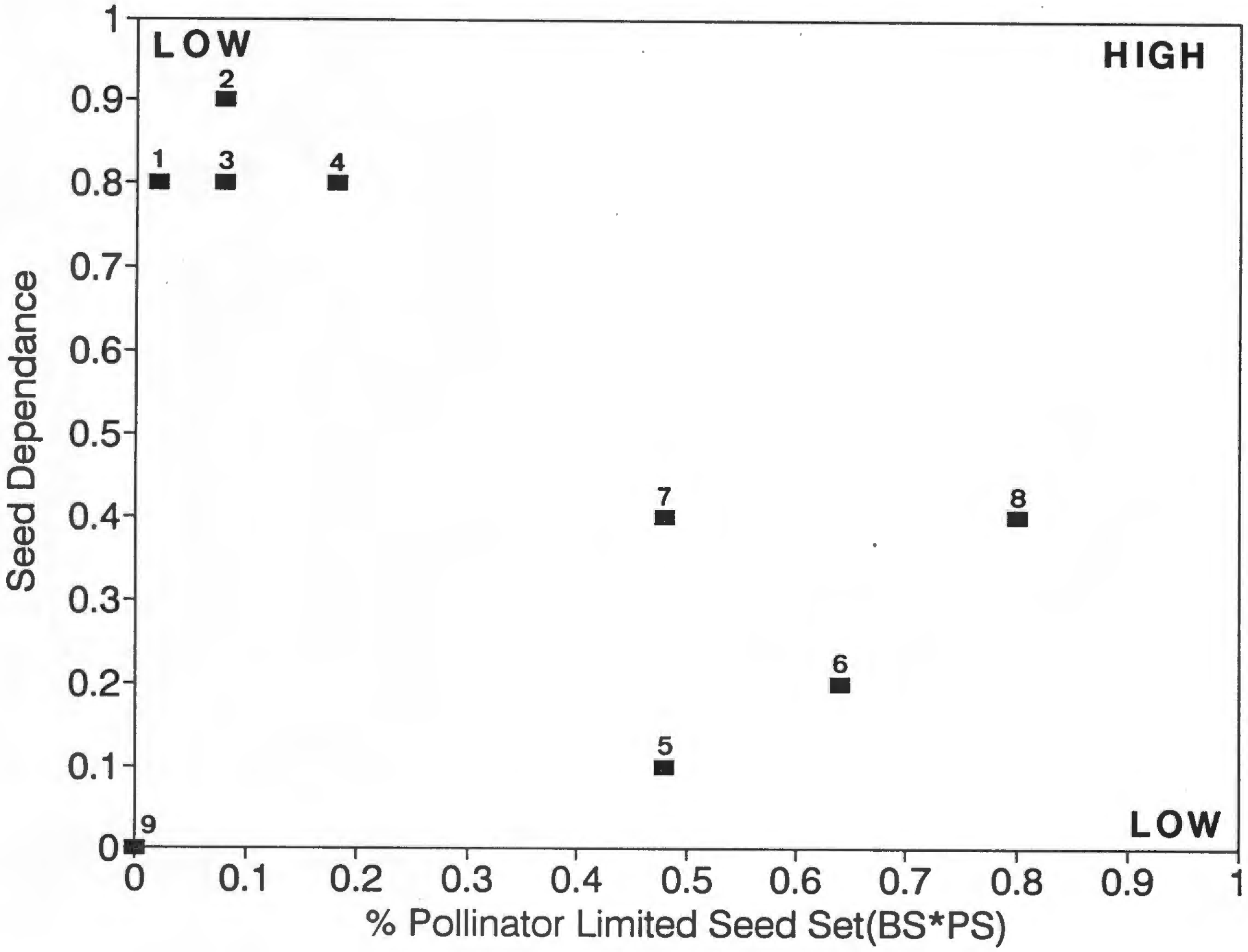

FIG 11. Plot of % pollinator limited seed set against seed dependance as a measure of extinction risk in the absence of pollinators. 1 = *Arctotis calendula, Dorotheanthus bellidiformis, Ursinia cakilefolia, Heliophila variabilis, Cotula barbata* 2 = *Gorteria diffusa* 3 = *Arctotis fastuosa* 4 = *Osteospermum hyoseroides* 5 = *Ferraria ferrariola, Gladiolus equitans* 6 = *Pelargonium triste* 7 = *Babiana curviscapa* 8 = *Pelargonim incrassatum, Lapeirousia silenoides* 9 = *Oxalis sp.*

pattern. This study aimed to determine how plant and associated insect species composition varies between adjacent disturbed and natural areas; with a view to understanding plant extinction processes. The risk assessment model proposed by Bond (1993) was utilised to investigate whether differences between areas was caused by variation in reproductive mutualisms.

5.1.Compositional differences between the natural and disturbed sites.

Plant and insect species composition was found to differ remarkably, between the ploughed lands and adjacent natural areas at Skilpad Nature Reserve. Plant species diversity declines from sixteen common species in the natural area to only six common species in the lands (Table 1). The natural spring flowering community is comprised primarily of annuals and geophytes (Fig 2). The abandoned lands are devoid of geophytes except, an *Oxalis sp*, and the flora consists entirely of annuals. The results of this study showed a complete change in the insect pollinator community and therefor the potential for plant reproductive failure due to collapsed reproductive mutualisms. The natural site contained a variety of generalist insect visitors to spring flowering species (Table 4). These insect visitors were almost entirely absent from the ploughed lands. Instead small Tenebrionoid beetles dominated in this area; comprising more than 95% of insect visitors to *Ursinia* growing in the disturbed lands (Fig 5b, 6b, 7b).

Insect diversity and abundance is known to decrease with decreasing habitat size and heterogeneity (Klein, 1989). Particular animal pollinators may decline, disappear or, in the case of species which thrive in an anthropogenic matrix, increase in abundance (Powell and Powell, 1987; Aizen and Feinsinger, 1994). The low insect diversity in these abandoned lands is intriguing firstly, since these two sites are less than 30m apart which implies that insects can easily traverse between the two sites. Janzen (1987) has similarly noted a decline in insect diversity between heavily farmed and natural areas which are less than 100m apart. Secondly the mass displays of *Ursinia* flowers would be expected to attract insects to the area. Possible reasons for the abrupt turnover in insect assemblages between the ploughed lands and veld remnants were not studied. However, the important point is that mass displays are unsuitable habitats for most of the native insect species visiting flowers.

5.2. The role of reproductive mutualisms

Could these changes in insect assemblages influence floral composition of the disturbed and natural sites? The absence of geophytes from the abandoned lands and dominance of annuals in this area suggests that these two groups may differ in their possession of certain traits.

Pollinator specificity varies between the disturbed and undisturbed sites. The annual species all seemed to have generalist flowers; which are visited by a variety of unrelated insects, mainly beetles and flies (Table 4). In the South-West Cape, beetles are frequent visitors to many Asteraceae species, which may be considered as typical "beetle flowers" (Scholtz and Holme, 1985; Whitehead et al., 1987). It has further been suggested that monkey beetles may play an important role in pollination of the large annual Namaqualand floral displays (Scholtz & Holme, 1985). The virtual absence of these beetles in the mass displays of *Ursinia*, however, refute this suggestion. It should be stressed that insect visitors can not automatically be regarded as pollinators. For example the Tenebrionids common in the disturbed lands had smooth bodies with no hairs and appear to be very poor pollinators.

In contrast the geophytes possess specialist flowers; their floral biology (Table 3) only permits pollination by certain highly specialised insects eg long-proboscid flies are the exclusive pollinators of *Lapeirousia, Pelargonium incrassatum* (Vogel, 1954). Dependence on a visitor type that is not abundant or always available, as is the case for most of the geophytes in this natural community, makes these species much more susceptible to pollinator failure than species with more diverse floral visitors (Motten, 1986). Jennersten (1988) has elegantly shown the negative effects of habitat fragmentation on visitation and seed set of the butterfly adapted *Dianthus deltoides*, due to the absence of its specialist pollinator.

A knowledge of plant breeding systems is of major importance in assessing dependence on pollinators (Bond, 1993). However, little work has been done on plant breeding systems in Southern Africa (Steiner, 1987). In this study, a distinct dichotomy in breeding systems was found to exist between the annuals and the geophytes. The annuals were all self-compatible (autogamous or geitonogamous)(Table 5), except *Osteospermum hyoseroides* which has unisexual florets and is consequently obligately xenogamous (Table 3). In contrast, the geophytes were all protandrous and self-incompatible. (Table 5). Both the geophytes and annuals generally have a low fruit set (Table 5). In the geophytes, this low fruit set could be prompted by low resources resulting in fruit or seed abortion or by a shortage of pollinators (Bierzychudek, 1981). Hand-pollination studies are, however, necessary to differentiate between these two causes. Johnson (1992) has shown that many geophytes display pollinator limited seed set. The Asteraceae also display low fruit set per capitula but this is attributed to resource limitations by the plant (Stephenson, 1981)

Plants are able to escape from environmental uncertainty by either a) the possession of underground storage organs such as: bulbs and corms or b) having persistent seed banks (Richards, 1985). Geophytes utilise the former option while annuals and perennial often possess seed banks (Moll and McKenzie, 1994). Geophytes are thus less dependant on seeds for survival and the small fleshy seeds of *Babiana curviscapa, Ferraria ferrariola* and *Lapeirousia silenoides*; suggests that they lack seed dormancy and don't form seed banks. These geophytic species may thus need to germinate soon after the seeds are released.

Le Roux and Schelpe (1988) state that a characteristic of most Namaqualand plants is their prolific production of seed and the presence of seed stores in the soil, however, it is uncertain whether all the species in this study area are able to produce seed banks. The presence of annual seed banks is supported by Van Rooyen et al (1979b), who found that an incredible number of seedlings could germinate in a metre squared patch after heavy rains: *Cotula barbata* produced 1158 seedlings in a m^2 plot. In addition annual species variation in mass flowering is only possible if seed banks are present. The dependence of a species on seeds for survival and recolonisation is determined by the amount of seeds which it produces, its ability to propagate vegetatively and also longevity (Fig 10).

The majority of the flowering plants at the Skilpad study site were wind dispersed (Table 6), and consequently have dispersal specificity (DS) values of zero (Table 7). *Lapeirousia silenoides, Ferraria ferrariola* and *Babiana curviscapa* all have slightly fleshy seeds which require some sort of biotic dispersal vector. *Gorteria diffusa* has synaptospermous diaspores (Table 6); which require external transport by a biotic dipersal vector. These species are consequently dependant on dispersal mutualisms for recruitment. However, generally, dispersal mutualisms are of minor importance in this semi-arid environment (compare with Howe, 1984; tropical dispersal mutualisms and Boucher, 1985 ant-dispersal mutualisms).

For many species, it is dispersal limitations, rather than survival capacity that restricts their distribution (Crawford, 1989). Dispersal dependence is, however a problematic section of this model since the dependence on dispersal for survival and recruitment depends on specific microsite requirements as well as germination cues. Both of these attributes are unknown, or only speculated, for the majority of these Namaqualand species. *Babiana* and *Ferraria* were always found growing near or under shrubs in the natural site. Does this mean that they will only survive if they are dispersed to these specific microsites? The importance of dispersal for annuals is also speculative since little is known about their germination requirements and thus their dependance on dispersal for recruitment.

5.3. Predictions made by the vulnerability index

The incorporation of the above-mentioned traits into a vulnerability index results in certain species being considered vulnerable to extinction, in the absence of their mutualist partners. I have already emphasised the fact that dispersal mutualisms of this semi-arid community, seem to be less important than those involving pollinators. The predictions concerning species vulnerability will thus focus primarily on the breakdown of pollination mutualisms. Geophytes and annuals in the area differ in all traits except dispersal, and the vulnerability index consequently makes different predictions for these two life-forms.

The model predicts that species which are most dependant on pollination mutualisms will be at the greatest risk of extinction in the face of disturbance. These species should be entirely dependant on seed set for reproduction and survival; as the ability to propagate vegetatively promotes survival in the absence of pollinators. Steiner (1993), found that the rare fynbos shrub *Ixianthes* continues to persist, by vegetative propogation, even though its specialist bee is thought to be locally extinct. These vulnerable species should additionally be short-lived as longevity confers survival advantages to the species concerned. According to this criteria the model predicts that, amongst the annuals, the autogamous species will be at a far lower risk of extinction than the species which rely on generalist insects for geitonogamy or xenogamy. Thus *Osteospermum* is predicted to be at the highest risk of extinction among the annuals. *Arctotis fastuosa* and *Gorteria diffusa* are also predicted to be slightly vulnerable to extinction. *Ursinia, Cotula,* and *Arctotheca* are predicted to be at the lowest risk of extinction (Table 7, Fig 11).

How does this compare with the observed species composition in the disturbed lands? The predictions made by the model are congruent with the situation in the lands: all the vulnerable species are entirely absent from the area and the "safe" (autogamous) species are common at this site. The scarcity of generalist insects in the disturbed lands suggests that *Osteospermum, Gorteria* and *Arctotheca* may be unable to inhabit the disturbed site due to the absence of their pollinators.

The geophytes which inhabit the natural site are mostly specialist species which depend on specific insects for successful pollination, except for *Ferraria* which depends on flies for pollination (Vogel, 1954). The absence of such specialist pollinators from the disturbed site suggests that all of these geophytic species should be vulnerable to extinction. However, the model proposes that longevity and or vegetative propagation may enhance the chances of survival should insect mutualisms breakdown; by reducing the dependence on seeds for survival. Geophyte size represents a crude estimate of life-span in this study. The large corm of *Pelargonium triste* thus places this species at a low risk of extinction (Table 7, Fig 10). In addition the ability of *Ferraria* and *Gladiolus* to propagate vegetatively reduces their risk of extinction in the absence of insect pollinators. The model predicts that the most vulnerable geophytic species, in terms of mutualism failure are: *Lapeirousia, Babiana* and *Pelargonium incrassatum*. Monitoring of these species populations should be useful in determing whether agricultural activities are altering insect pollinator assemblages, which in turn depend on plant species.

5.4. The ambiguous role of colonisation

A criticism of this risk assessment model is that it does not incorporate the importance of recolonisation of disturbed areas but only stresses the importance of survival. Population survival, of seed dependant species, in disturbed environments may depend on the recolonisation of habitat patches that have experienced extinction (Fahrig and Merriam, 1992). Dispersal and colonisation can act in a founder capacity once local extinction has occurred or as a means of supplementing populations which are facing local extinction (Gonzalez-Andujar and Perry, 1993). Vegetative propagation and longevity do not aid in recolonisation of a disturbed area. If the term SD (dependence on seeds for persistence) is replaced by SC (seed dependance in terms of colonisation success); the importance of vegetative propagation and longevity in assuring the survival of a species diminishes drastically. The geophytes would then all be at a high risk of extinction; since they all require seeds for recolonisation. The extremely low natural seed set of these species (Table 5), as well as the apparent absence of specialist pollinator guilds, suggests that they would be extremely vulnerable. This prediction would then be in agreement with the findings from the ploughed lands (all geophytes are absent from the site). However, an alternative, and possibly more plausible explanation exists for the local extinction of geophytes in these disturbed areas: the lack of geophyte seed banks. Ploughing may eliminate all geophytic plants and the lack of seed banks would consequently result in extremely low rates of recolonistion into the area.

The risk assessment model proposed by Bond (1993) makes useful predictions for annual species. However, in the case of the geophytes, reproductive barriers to colonisation of old lands by breakdown in pollination mutualisms may not be the primal cause of local extinction. Further research is required on the presence or absence of seed banks in all these flowering species, seed dormancies and germination cues also need to be investigated for these species before reproductive mutualisms are considered the over-riding factors affecting distribution patterns. In addition little is known about the colonisation strategies of these flowering species.

Colonisation prohably plays a vital role in determining species composition of the disturbed site. Colonisation success involves an array of factors (Harrison, 1991) which need to be evaluated. A possible apprach to investigating the importance of colonisation could involve ploughing an area of land and noting which species enter the area first as well as which species are good competitors. Lottery models could be incorporated into such an experiment. Similarly, the effect of spraying with pesticides on a tract of natural veld on insect and associated plant species composition could be investigated. Kevan (1975), has highlighted the impacts of herbicide and pesticide sprays on insect diversity and interrelated plant species. Such an experiment may clarify whether pollinator-plant interactions or other factors are more important in determine species composition.

5.5. Conservation implications of this study

The study has made two important findings. Firstly, ploughing eliminates all non-propagating geophytes from an area; although the causes of the local extinction are still unresolved. Geophytes take a long period to recolonise a disturbed area (longer than three years). This loss of geophytes has important consequences for conservation of natural areas which have a wealth of geophytic species. The effects of ploughing seem to contradict those of grazing. Niel Macgregor, a well known conservationist, combines intermittent grazing with "flower farming" near Nieeuwoudtville. The area is extremely rich in geophytic species and grazing appears to stimulate mass flowering of these bulbous species, however, virtually eliminating all annuals. It is possible that the removal of annuals reduces competition for resources and may consequently enhance vegetative propagation.

The second, important finding of this study was that pollinator diversity is dramatically reduced in these ploughed areas. Although the natural patches of vegetation are extremely close to the ploughed lands many insects do not enter the lands. This has implications for pollinator diversity in the whole reserve and for pollination in the area. The absence of specialist pollinator guilds at the natural site may be an indication of the effects of fragmentation of the area with the small patches of natural vegetation being incapable of supporting populations of pollinators. The implications of fragmentation on insect fauna has been stressed by many authors, however the effects on interrelated plant species constitutes a serious void in ecological research (Kevan, 1975). Although the mass-flower displays in the ploughed lands provide a useful income to the Reserve; ploughing of the lands, to encourage mass displays will restrict insect populations to island - like remnants of natural veld and promote local extinction through the fragmentation process. This may lead to a cascade of plant extinctions, of those species which are highly dependant on insects for seed set, survival and recolonisation.

5.6. CONCLUSION

This is the first time that it has been empirically demonstrated that species producing mass flower displays in Namaqualand do not require insects for pollination. The mass displays at Skilpad Nature Reserve were comprised exclusively by autogamous annuals; which consequently set seed independent of pollinator availability. Geophytes, which are abundant in the natural areas of the Reserve are completely absent in these ploughed fields. The failure of reproductive mutualisms due to changes in insect assemblages, may play an important role in the annual species composition of these disturbed areas. Annuals which rely on insects for pollination (*Arctotis fastuosa, Gorteria diffusa* and *Osteospermum hyoseroides*), were found to be absent from the disturbed sites suggesting that pollinators may be crucial to their survival in these areas. Dispersal mutualisms are apparently less important in this region due to the fact that most species have wind dispersed diaspores. The lack of data on germination requirements and seed banks of many of these species however makes it difficult to speculate on the degree of dependence on dispersal. Future studies investigating these factors would be extremely useful in this area. The absence of geophytes from the disturbed site is in agreement with the predictions of Bond's (1993) model, if the importance of recolonisation replaces the emphasis on persistence. However, this does not necessarily imply that pollination mutualisms are all important. The absence of seed banks in the majority of these geophytic species may also be the cause of their absence in these areas. This study has illustrated that the mass flower displays, for which Namaqualand is renowned, are devoid of insect visitors. This may result in local extinction of plant species which depend on these visitors for pollination. Since the object of creating a reserve is to maintain species diversity these mass displays should not be encouraged.

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Appendix 1a. List of most common shrubs inhabiting the natural site.

ASCLEPIADACEAE
Microloma sagittatum R.Br.

ASTERACEAE
Berkeya fruticosa (L.)Ehrh.
Chrysocoma ciliata L.
Didelta spinosa (L.f.)Ait.
Eriocephalus africanus L.
Osteospermum grandiflorum DC.
Pteronia incana *(Burm.)*

CAMPANULACEAE
Wahlenbergia oxyphylla *A.DC.*

ANACARDIACEAE
Rhus burchellii Sond.ex Engl.
Rhus incisa L.f.

SOLANACEAE
Solanum giftbergense Dun.
Lycium ferocissimum *Miers*

AIZOACEAE
Tetragonia macroptera Fenzl
Galenia africana L.

POLYGALACEAE
Nylandtia spinosa (L.)Dumort

FABACEAE
Indigofera heterophylla Thunb.
Lebeckia sericea Thunb.
Wiborgia minoptera E.Mey.

GERANIACEAE
Pelargonium praemorsum (Andr.)F.Dietr.

Appendix 1b. Raw data and averages of shrub density per m_2 for five transects in the natural site.

0	100	100	100	100
90	75	0	0	25
0	0	75	0	50
0	0	0	0	100
0	25	0	50	100
0	0	75	0	0
100	0	0	0	0
25	50	0	50	30
0	25	0	25	0
100	95	100	0	50
0	0	25	50	0
0	100	75	75	100
0	70	0	50	100
0	75	0	50	100
25	25	75	75	100
100	100	50	100	100
100	100	25	100	0
100	0	50	0	0
50	50	50	0	0
50	50	0	75	100
100	25	0	25	100
100	75	0	75	50
50	100	75	0	20
100	0	100	100	30
50	75	100	0	0
45.6	48.6	39	40	50.2

Table 3. Summary of floral biology characteristics for the 16 most common spring flowers growing at the natural site.

SPECIES	COLOUR	SIMPLE/ COMPLEX FLOWERS	SEXUAL SYSTEM: STRUCTUR OF CAPITULA/FLOWERS	LIFE FORM	PRESENT IN LAND/VELD/BOTH
STERACEAE					
A.calendula	Yellow	simple	Ray florets sterile Disc florets bisexual	Annual	B
A.fastuosa	Orange	simple	Ray florets female Disc florets bisexual	Annual	V
C.barbata	Yellow	simple	Ray florets absent Marginal florets female Central florets bisexual	Annual	B
D.sinuata	Orange	simple	Ray florets female/sterile Disc florets bisexual/male	Annual	L
G.diffusa sp.diffusa	Orange + green,black & white markings	simple	Ray florets sterile Disc florets bisexual	Annual	V
O.hyoseroides	Yellow	simple	Ray florets female Disc florets sterile/male	Annual	V
U.cakilefolia	Orange	simple	Ray florets neuter Disc florets bisexual	Annual	B
RASSIACEAE					
H.variabilis	White	simple	bisexual	Annual	B
ERANIACEAE					
P.incrassatum	Pink	complex	Bisexual, protandrous	Geophyte	V
P.triste	Creamy yellow	complex	Bisexual, protandrous	Geophyte	V
RIDACEAE					
B.curviscapa	Purple	complex	Bisexual, slight protandry	Geophyte	V
F.ferrariola	Pale blue-green	complex	Bisexual, protandrous	Geophyte	V
G.equitans	Brick red with lower perianth lobes Yellow-green & red tips	complex	Bisexual, protandrous	Geophyte	V
L.silenoides	Pink + cream markings & white perianth tube	complex	Bisexual	Geophyte	V
ESEMBRYANTHEMACEAE					
D.bellidiformis sp.hestermalensis	Pink-white	simple	Bisexual, protandrous	Annual	V
XALIDACEAE					
xalis sp.1	Yellow	simple	Bisexual, tristylous	Geophyte	B

Table 5. Breeding systems of spring flowering species growing at the natural site. The ability to set fruit in the absence of insects indicated either autogamy or geitonogamy. Failure to set seed in the absence of insect visitors indicates self-incompatability. The differences between natural and enclosed fruit set was investigated for each species by Mann-Whitney test. ** indicates significant differences at the 0.05 level. *** indicates significant differences at the 0.001 level. NS = Not significant difference.

PLANT SPECIES	TEST	PLANT (N)	TOTAL # OF FLOWERS	TOTAL # OF FRUIT	% FRUIT SET	AUTO-/GEITONOGAMY /NEITHER	Z
ASTERACEAE							
Arctotheca calendula	open enclosed	7 5	276 185	150 109	54.35 58.92	A	0.3320 NS
Arctotis fastuosa	open bagged	7 5	2320 1776	457 0	19.7 0	G	0.0021 **
Cotula barbata	open enclosed	6 9	345 201	55 43	15.94 21.39	A	0.1390 NS
Dimorphotheca sinuata	open enclosed	8 10	950 !	750	78.95	/	
Gorteria diffusa ssp. diffusa	open bagged	9 6	140 54	134 0	95.71 0	G	0.0008 ***
Osteospermum hyoseroides	open enclosed	6 6	288 288	212 0	73.61 0	A	0.0025 **
Ursinia cakilefolia	open enclosed	7 5	1110 870	405 50	36.49 5.75	A	0.0027 **
BRASSIACEAE							
Heliophila variabilis	open enclosed	10 10	204 160	204 160	100 100	A	0.3173 NS
GERANIACEAE							
Pelargonium incrassatum	open bagged	6 5	380 232	66 0	17.37 0	/	0.0055 **
Pelargonium triste	open bagged	6 5	51 31	8 0	15.69 0	/	0.0169 **
IRIDACEAE							
Babiana curviscapa	open bagged	7 7	82 121	7 0	8.54 0	/	0.00056 **
Ferraria ferrariola	open bagged	6 5	63 54	25 0	39.68 0	/	0.00379 **
Gladiolus equitans	open bagged	7 8	29 32	19 0	65.52 0	/	0.0004 ***
Lapeirousia silenoides	open bagged	7 6	135 110	25 0	18.52 0	/	0.00207 **
MESEMBRYANTHEMACEAE							
Dorotheanthus bellidiformis ssp. hestermalensis	open enclosed	18 12	32 15	32 15	100 100	A	0.3179 NS

* Oxalis species were assumed not to set seed without insects

! Plants died after transplanting

Subject: Mail failed, returning to sender

Sue

Could you possibly try and track down Roweena's thesis and find the missing tables for this student? Maybe I should check them before we fax them.

Thanks.

William

Received: from SpoolDir by SCIENTIA (Mercury 1.31); 4 Jul 97 11:23:00
From: "Claudia Ueckermann" <N9415610@scientia.up.ac.za>
Organization: University of Pretoria
To: wbond@botzoo.uct.ac.za
Date: Fri, 4 Jul 1997 11:22:58 GMT+2
Subject: Inquiry about pollination at Skilpad
Priority: normal
X-mailer: Pegasus Mail for Windows (v2.01)
Message-ID: <4BD5E66C91@scientia.up.ac.za>

Prof. Bond,

I am student at the University of Pretoria and am doing my honours project with dr.Gretel van Rooyen on the pollination of a few Namaqualand flowering plants.

I found the study done by Rowena Smuts (1994) under your supervision very interesting and insightful. We have a copy of the summary report for the SANF as well as the complete report named "Is local plant extinction a product of mutualism breakdown? A case study of the Namaqualand spring flora" which describes her stury and results. However, one page is missing. The missing page contains tables 2 and 3 which include summary of the floral biology descriptions of the species that she observed, and it would be very helpful if you could send this to me.
Yours sincerely
Claudia Ueckermann

Our fax number is: 43 2184
Or E-mail me at: n9415610@.scientia.up.ac.za
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Attention: Claudia Ueckermann

Dear Claudia
Here are tables two and three from the honours thesis of Rowena Smuts, as requested. I have also included table 5 as this is the critical table to the thesis, just incase it was missing too. Sorry about the delay.

Hope all goes well with your work and please contact us again if there is anything we can help with.

Yours sincerely

Sue van Rensburg (on behalf of Prof. W.J. Bond)

Table 2. Spring floral composition of the natural and disturbed study sites at Skilpad Nature Reserve.

Natural site

ASTERACEAE
Arctotheca calendula (L.) Levyns.
Arctotis fastuosa (L.) Jacq.
Cotula barbata (L.) DC.
Gorteria difussa ssp diffusa (L.) Thunb.
Osteospermum hyoseroides (L.)(DC.) T. Norl.
Ursinia cakilefolia (DC.)

BRASSIACEAE
Heliophila variabilis (L.) Burch. ex DC.

GERANIACEAE
Pelargonium incrassatum (Andr.) Sims
Pelargonium triste (L.)L'Hent

IRIDACEAE
Babiana curviscapa G.J. Lewis
Ferraria ferrariola (Jacq.) Willd
Gladiolus equitans Thunb.
Lapeirousia silenoides (Jacq.) Ker-Grawl

MESEMBRYANTHEMACEAE
Dorotheanthus bellidiformis ssp. hestermalensis (Burm. F.) N.E. BR. Ilenf. & Struck

OXALIDACEAE
Oxalis sp

Disturbed site

Arctotheca calendula
Cotula barbata
Dimorphotheca sinuata
Ursinia cakilefolia
Heliophila variabilis
Oxalis sp.

Appendix 2. Summary of Geophyte data.

SPECIES	NUMBER OF CORMS	CORM SIZE cubic cm	DEPTH BELOW GROUND(cm)	VEGETATIVE PROPOGATION
B.curviscapa	1	7.1	7.09	N
F.ferrariola	4	14.7	14.718	Y
G.equitans	2	5.9	4.85	Y
L.silenoides	1	0.4	1.66	N
Oxalis sp	3.4	0.03	1.64	Y
P.incrassatum	1	2.5	1.15	N
P.triste	1	158	16	N