
Effects of Habitat Fragmentation on Pollinator Diversity and Plant Reproductive Success in Renosterveld Shrublands of South Africa

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Abstract: We examined the effects of habitat fragmentation on the pollinator diversity and reproductive success of seven perennial plant species in renosterveld shrublands in South Africa. We sampled pollinators in small (0.5–2 ha), medium (3–10 ha), and large (>30 ha) habitat fragments during the peak flowering period in spring and summer. We also compared fruit set and seed set in the seven plant species on different-sized fragments. Hand-pollinated controls were used to determine pollination deficits in three species. Seed-germination studies were done on two species to determine the effect of reduced seed set on reproductive output. Overall, the species richness of bees, flies, and butterflies did not vary significantly among different-sized fragments. However, the abundance of particular species of bees and monkey beetles (Scarabaeidae: Hopliini) was significantly affected by fragment size, together with other factors such as vegetation cover and the ratio of grass to shrubs. Fragment size and distance to large remnants of vegetation had a significant influence on seed or fruit set in four of the seven plant species examined. One species failed to set any seed in small- and medium-sized fragments. Comparisons of fruit and seed set among hand-pollinated and naturally pollinated plants confirmed that seed set was pollinator-limited in the orchid *Pterygodium catholicum*. Our results suggest that perennial plant species respond in different ways to fragmentation, and that populations on small fragments do not always experience pollination deficits. Existing classifications of pollination systems, in relation to their vulnerability to fragmentation, do not adequately explain our results. We argue that there needs to be a greater focus on the habitat requirements of pollinators to predict the effects of habitat fragmentation on pollination systems and plant reproductive success.

Efectos de la Fragmentación del Hábitat sobre la Diversidad de Polinizadores y el Éxito Reproductivo de Plantas en Matorrales Renosterveld (Suráfrica)

Resumen: Examinamos los efectos de la fragmentación del hábitat sobre la diversidad de polinizadores y el éxito reproductivo de siete especies de plantas perennes en matorrales renosterveld en Suráfrica. Muestreamos polinizadores en fragmentos de hábitat pequeños (0.5–2 ha), medianos (3–10 ha) y grandes (>30 ha) durante el período de máxima floración en primavera y verano. También comparamos el conjunto de frutos y el conjunto de semillas en las siete especies de plantas en fragmentos de diferente tamaño. Se utilizaron controles polinizados manualmente para determinar el déficit de polinización en tres especies. Se realizaron estudios de germinación de semillas en dos especies para determinar el efecto de la reducción del conjunto de semillas en la reproducción. La riqueza total de especies de abejas, moscas y mariposas no varió perceptiblemente entre fragmentos de diferentes tamaños. Sin embargo, la abundancia de especies particulares de abejas y de escarabajos mono (Scarabaeidae: Hopliini) fue afectada significativamente por el tamaño del fragmento junto con otros factores como la cubierta de vegetación y la proporción pasto - arbustos. El tamaño del fragmento y la distancia a remanentes grandes de vegetación tuvieron una influencia significativa en el con-

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junto de semillas o frutos en cuatro de las siete especies examinadas. Una especie no pudo fijar ninguna semilla en fragmentos pequeños ni medianos. Las comparaciones del conjunto de frutos y de semillas entre las plantas polinizadas manual y naturalmente confirmaron que el conjunto de semillas era limitado por el polinizador en la orquídea Pterygodium catholicum. Nuestros resultados sugieren que las especies de plantas perennes responden de diversas maneras a la fragmentación, y que las poblaciones en fragmentos pequeños no siempre experimentan déficit de polinización. Las clasificaciones existentes de los sistemas de la polinización, en lo referente a su vulnerabilidad a la fragmentación, no explican adecuadamente nuestros resultados. Discutimos que se necesita mayor atención en los requerimientos de hábitat de los polinizadores para predecir los efectos de la fragmentación del hábitat en sistemas de polinización y en el éxito reproductivo de plantas.

Introduction

The pervasive nature of habitat fragmentation makes it one of the most important factors threatening the survival of plant and animal species (Usher 1987; Saunders et al. 1991). Fragment size and the degree of isolation have been identified as key determinants of species diversity in fragmented systems (Wilcox & Murphy 1985; Gilpin & Soulé 1986; Saunders et al. 1991; Haila et al. 1993). Contrary to this general trend, studies of vascular plants in fragmented habitats have regularly shown a poor correlation between fragment size, or isolation, and species diversity (Haila et al. 1993; Kemper 1997; Köchy & Rydin 1997; Kemper et al. 1999). These results imply that plants may be more resilient to habitat fragmentation than other taxa (Köchy & Rydin 1997). However, plant responses to decreasing habitat area and increasing isolation may be obscured by the persistence of perennial species that can survive for long periods because of persistent seed banks or perennial vegetative structures (Aizen & Feinsinger 1994a; Bond 1994; Bronstein 1995). Measures of the effect of habitat fragmentation on plant diversity should therefore take into account the viability of remnant populations of perennial plants.

The collapse of pollinator mutualisms, with a resultant decrease in plant reproduction, has been identified as one of the potential consequences of habitat fragmentation (Lamont et al. 1993; Aizen & Feinsinger 1994a, 1994b; Kearns & Inouye 1997; Allen-Wardell et al. 1998). Although evolutionary theory suggests that plants should alter their allocation of resources to sexual reproduction to minimize the incidence of pollination deficits (Thompson 2001), these responses may not occur within the ecological time frames associated with habitat fragmentation. Severe pollination deficits may therefore occur as a result of recent declines in pollinators (Burd 1994; Thompson 2001). The local extinction of plant populations in fragmented landscapes may be the end result of complex processes in which some populations persist as nonreproducing individuals that will eventually die whereas others will survive as a result of selection for self-compatibility and self-pollination (Allen-Wardell et al. 1998).

We examined the effects of fragmentation on insect-pollinator diversity and plant reproductive success in renosterveld shrublands, a highly threatened vegetation type in the species-rich Cape Floral Region of South Africa (Rebelo 1992). We sought to determine (1) how the diversity of insect pollinators is affected by habitat fragmentation, (2) whether perennial plant species experience pollination deficits as a result of habitat fragmentation, and (3) how pollinator limitation affects reproduction in perennial plant species. Our initial hypothesis was that the diversity of insect pollinators would be lower on small and isolated fragments than on large patches of vegetation, and that the insect fauna on small fragments would decline further because of the effects of insecticide drift from surrounding croplands. We therefore expected plant populations on small fragments to experience more frequent pollination deficits and lower viability than populations on large fragments. We focused on seven perennial plant species with a variety of pollination systems. We discuss our results in the context of current knowledge of pollination systems in fragmented landscapes and in terms of the effects of farming practices on the conservation of renosterveld vegetation.

Study Area

Renosterveld shrublands are characterized by the presence of low-growing, sclerophyllous shrubs, varying grass cover, and a large number of spring-flowering geophytes. These shrublands occur on the more nutrient-rich tillite and shale substrates of the Cape Floristic Region, and they have been substantially transformed by crop cultivation over the past 150 years (Rebelo 1992; Kemper et al. 1999). Less than 15% of original renosterveld vegetation remains (Rebelo 1992), and most of it is habitat remnants surrounded by cereal crops.

Our study site was located on the farm Fairfield, west of Napier in the Western Cape province of South Africa, where 4900 ha is situated on shale soils that were covered by renosterveld vegetation prior to conversion to agriculture. The topography of the area is characterized

by gently undulating hills with a maximum difference in elevation of <100 m across the study site. Fairfield has been owned by the van der Bijl family since 1853, and the pattern of land use has remained relatively unchanged since 1945 (P.K. van der Bijl, personal communication). Of the landscape originally covered by renosterveld, 80% has been converted to wheat production, 3% has been invaded by alien vegetation (*Acacia* spp.), and 1% is roads and farmhouses.

There were 57 remnants of renosterveld vegetation on Fairfield, ranging in size from <1 ha to >100 ha. Larger remnants of renosterveld were retained for grazing sheep and have been periodically burned to encourage grasses. Smaller remnants (<10 ha) occurred mostly in areas that were difficult to plow, such as rocky outcrops, steeper slopes, drainage lines, and road verges. Smaller remnants were not managed in any specific way and were typically treated as part of the wheat field (i.e., they were affected by annual burns to remove wheat stubble and were subjected to aerial sprays of fungicide and insecticide).

We classified all the fragments according to their size, vegetation cover, slope, aspect, and soil type as the basis for a stratified sampling approach. At least 24 fragments of varying sizes incorporated a south-facing aspect, gentle slope, and duplex shale soils. We restricted our sampling to fixed areas within fragments that had these characteristics. Fragments were ranked into three broad size classes: large (>30 ha), medium (3–10 ha), and small (0.5–2 ha). We identified eight fragments from each size class. For each fragment, we measured the area, perimeter, distance to the nearest fragment, and distance to the nearest large patch of renosterveld (>30 ha). Large fragments represented the largest tracts of renosterveld still in existence and were therefore the nearest equivalents to a “mainland.”

Methods

Distribution and Abundance of Insect Pollinators

We used circular yellow pans to trap insect pollinators. The pans (20 cm in diameter), were filled with water and detergent (30 drops dishwashing liquid/L water) and left out for 3 days. Each trap site contained four traps arranged in a square 10 m apart. Traps were set up in five remnants from each size class (large, medium, and small). We set traps on two separate occasions (11–14 October and 8–11 November 1994), representing the peak and end of the same flowering season. At the end of each trapping session, we removed insects from the traps and sorted them into taxonomic groups. For each trap site, we measured rockiness (percent area with exposed rocks), total vegetation cover, and percent grass cover. We made a distinction between grass cover and to-

tal vegetation cover, because grasses and shrubs were dominant in different parts of the landscape and represent different habitats and floral resources for pollinators.

Using one-way analysis of variance (ANOVA) we compared pollinator diversity between small, medium, and large fragments. Separate analyses were carried out for each sampling date. Similarity in insect-species composition between fragments was determined by the Morista-Horn index. We also analyzed pollinator diversity in relation to fragment characteristics—size, neighbor distance, distance to mainland, perimeter, rockiness, vegetation cover, grass cover—based on species richness, the Brillouin index, and Shannon’s diversity index. Multiple-regression models (ordinary least-squared, Unistat) were used to identify significant variables.

Pollinator Limitation and Reproductive Success

During the spring flowering seasons of 1994 and 1995 (September to November), we compared the reproductive success of seven species of perennial plants (mostly geophytes) between large and small habitat fragments. The plants studied were *Babiana ambigua* (Iridaceae), *Berkheya armata* (Asteraceae), *Cyanella lutea* (Tecophilaeaceae), *Gladiolus liliaceus* (Iridaceae), *Ornithogalum thyrsooides* (Hyacinthaceae), *Pterygodium catholicum* (Orchidaceae), and *Trachyandra hirsuta* (Asphodelaceae). We chose these species because they are typical examples of herbaceous perennials in renosterveld shrublands and represent a range of pollination systems. During the course of our experiments, we identified potential pollinators for these plants, but no exclusion experiments were undertaken. Three different sets of treatments and observations were carried out with these seven species. It was not possible to include all species in all treatments because of the low numbers of plants in some fragments.

At the start of flowering, a minimum of 10 plants from each species was marked, and these were monitored throughout the flowering season until they set fruit or seed. With the exception of *B. armata*, which has a capitate inflorescence, we counted the number of flowers present on each inflorescence so that fruit set could be related to the original number of flowers. At the end of the flowering season, infructescences from all the marked plants were collected before seeds or fruits could be dispersed, and the number of fruits or seeds was counted. The observations were repeated on five large habitat fragments and five small ones. In the case of *B. ambigua* and *O. thyrsooides*, data were also collected from five medium-sized fragments. Data were compared between fragment size classes with analysis of variance (ANOVA). There was some variation in the size and characteristics of fragments within each size class. Therefore, we used multiple-regression models to determine whether fragment size, perimeter, distance to

mainland, nearest-neighbor distance, and pollinator-species diversity had an effect on fruit or seed set.

To distinguish poor seed set due to pollinator limitation from other possible causes, we hand-pollinated flowers of *P. catholicum*, *O. thyrsooides*, *B. ambigua*, and *G. liliaceus*. Pollen from conspecific plants at the site was dusted onto the stigmata of 10 plants from each species. All the flowers on the inflorescence ready for pollination were treated. These plants were monitored until seed or fruit set, then the infructescences were removed and the fruits (and in some cases seeds) were counted. An equal number of plants were left untreated as controls. Treatment and control plants were taken from the same area within the habitat fragment and had the same number of flowers on the inflorescence. In the case of *O. thyrsooides* and *B. ambigua*, unopened flower buds were removed from the inflorescence of both hand-pollinated and control plants. The experiment was replicated on five small and large fragments, and on medium fragments for *O. thyrsooides*.

The percent germination of apparently viable seeds from different field treatments was tested for *O. thyrsooides* and *B. ambigua*. For each species, 100 viable (plump) seeds from each pollination treatment in each fragment were collected, divided into four lots of 25 seeds each, and incubated in petri dishes with 2.5 mL of water containing 0.075% Benlate fungicide. If there were too few seeds available from any one site, as was the case for some *B. ambigua* populations, all the seeds in the population were used. Petri dishes were incubated under a controlled dark/light regime of 10°/20° C and 14/10 hours to simulate early spring conditions. Moisture levels were kept constant throughout the experiment. Germination was confirmed by the appearance of the radicle, and seeds that had not germinated after 2 months were opened to determine whether there was an embryo present. We used the proportion of seeds that germinated as the measure of germination success, and we compared arcsin-transformed data with a one-way ANOVA.

Results

Pollinator Diversity and Abundance

Thirty-six insect species (2734 individuals) from known pollinator guilds were collected from traps. The most diverse pollinator taxa were monkey beetles (Scarabaeidae: Rutelinae, 8 species), bees (13 species of Halictidae, 3 Anthophoridae, 2 Colletidae and *Apis mellifera capensis*), and butterflies and moths (Satyridae, *Pseudonympha trimenii*; Pieridae, *Colias electo electo*; Ctenuchidae, *Syntomis cerbera*). Other beetles (Mordellidae and Buprestidae) and wasps (Tiphidae and Masaridae) made up the remainder.

Total species richness for pollinators from both sam-

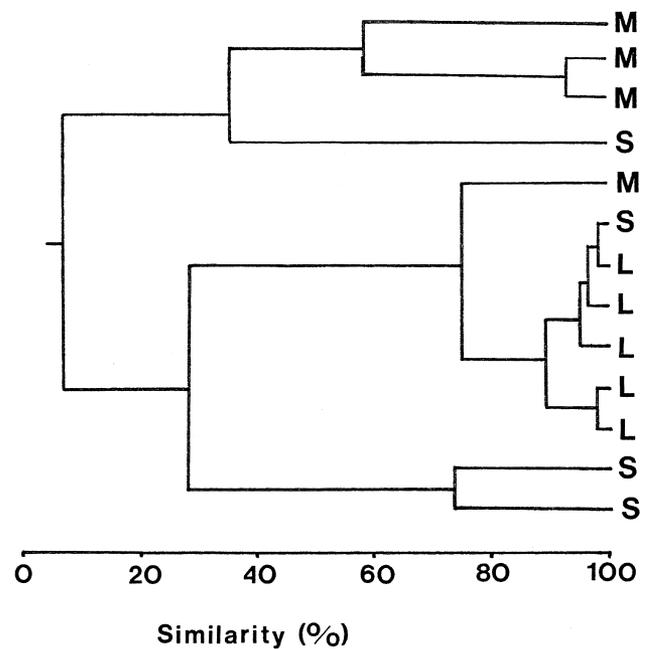


Figure 1. Similarity in species composition (based on the Morista-Horn index) for monkey beetles (Scarabaeidae: Hopliini) collected from traps on small (S), medium-sized (M), and large (L) fragments of renosterveld vegetation.

ple dates was slightly greater in small fragments ($n = 28$) than in either medium-sized ($n = 24$) or large fragments ($n = 21$), but none of these differences were significant (ANOVA, $F_{2,12} = 0.063$, $p > 0.5$). There was also no clear pattern of similarity in pollinator-species composition (Morista-Horn index) between fragments of different sizes. When the main taxa were analyzed separately, however, the species composition of monkey beetles was most similar among fragments of the same size (Fig. 1). A plot of common species—species that occurred in fragments from all size classes—versus those found in only one size class or those unique to one fragment (Fig. 2) suggests that the majority of species occurred in fragments from all size classes. Only four fragments contained unique species (one species in each fragment; Fig. 2), and nine fragments contained either one or two species restricted to fragments within the same size class (Fig. 2). Comparisons of Shannon diversity indices showed no significant differences between fragment sizes ($p > 0.1$).

Multiple-regression models, initially with fragment size, perimeter, distance to the mainland, nearest-neighbor distance, percent rockiness, percent vegetation cover, and percent grass cover, showed that percent vegetation cover and percent grass cover were the only significant variables in regressions with total pollinator species richness (ANOVA of regression, $F_{5,9} =$

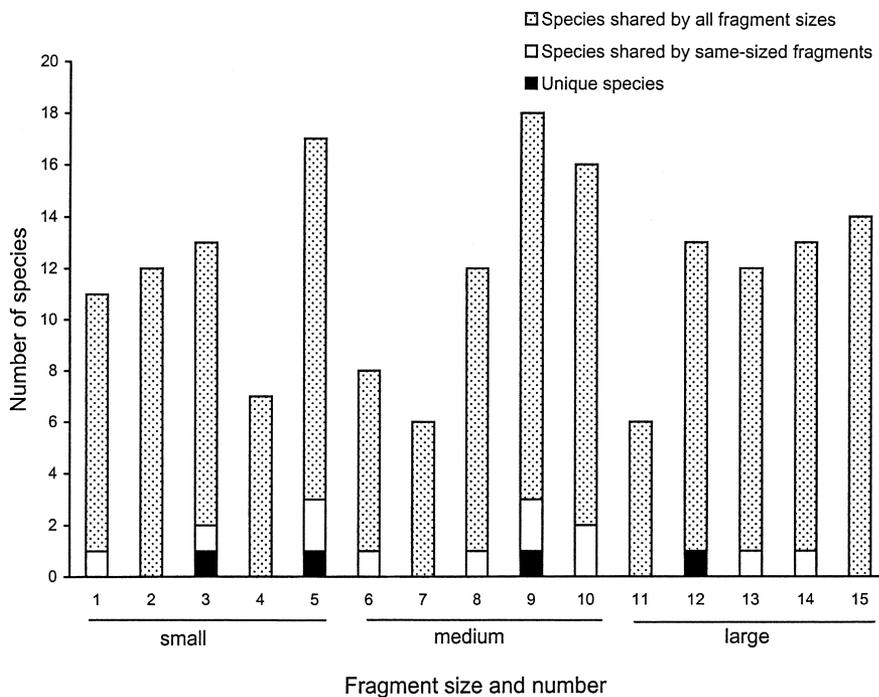


Figure 2. Number of insect pollinator species collected from traps set in small, medium-sized, and large fragments of renosterveld (five replicates of each size class). Each column represents a single fragment and depicts the number of unique species, species shared by sites within the same size class, and those species found on fragments in all size classes.

21.9, $p < 0.01$), the Brillouin index of pollinator diversity (ANOVA, $F_{5,9} = 61.1$, $p < 0.01$), and the Shannon index (ANOVA, $F_{5,9} = 62.9$, $p < 0.01$). Differences in vegetation cover and grass cover accounted for >90 % of the variation in all the regression models, with high vegetation cover and high grass cover associated with low insect diversity. When the Brillouin index was used, fragment size emerged as a third variable ($p < 0.05$) that accounted for <10% of variation in pollinator diversity, with lower evenness values on small fragments.

Several pollinator species appeared to be more common in fragments from a particular size class, but only four species showed a statistically significant difference in abundance. The monkey beetle, *Pachynema* sp.1, was consistently more abundant in large fragments ($F_{2,12} = 4.38$, $p < 0.05$), whereas *Dichelus* sp.1 was more abundant in small fragments ($F_{2,12} = 5.36$, $p < 0.05$). Two

other groups of beetles (Coleoptera: Mordellidae and Buprestidae) were significantly more common in large fragments ($p < 0.05$). Multiple-regression analyses based on other parameters in addition to fragment size showed that percent vegetation cover, distance to mainland, and percent grass cover were the only significant variables influencing the abundance of *Pachynema* sp.1 ($p < 0.01$, $R^2 = 0.53$). High abundance of *Pachynema* sp.1 was associated with high vegetation cover, low grass cover, and short distances to the mainland. In contrast, high numbers of *Dichelus* sp.1 were associated with high percent grass cover, high rockiness, and short distances to the mainland ($p < 0.01$, $R^2 = 0.38$). Another monkey beetle, *Peritrychia* sp.1, was most abundant in large fragments close to the mainland ($p < 0.05$, $R^2 = 0.45$), and the combined abundance of all bee species was highest in fragments with low grass cover and high rockiness ($p < 0.05$, $R^2 = 0.35$).

Table 1. Comparison of fruit set in seven perennial plant species from small, medium-sized, and large fragments in renosterveld shrublands.

Species	Mean (SE) fruit set						
	small	n	medium	n	large	n	p*
<i>Babiana ambigua</i>	76 (8.2)	20	59 (4.9)	20	27 (2.3)	20	<0.01
<i>Berkbeya armata</i>	11.06 (4.7)	40	—	—	8.03 (4.3)	46	ns
<i>Cyanella lutea</i>	42.6 (9.2)	49	—	—	48.1 (1.8)	64	ns
<i>Gladiolus liliaceus</i>	89 (4.2)	67	—	—	96.7 (2.01)	32	ns
<i>Ornithogalum thyrsoides</i>	52.8 (17.2)	24	62.1 (12.5)	24	57.4 (9.4)	24	ns
<i>Pterygodium catholicum</i>	0	213	0	—	14.3 (7.4)	240	<0.05
<i>Trachyandra birsuta</i>	25.3 (5.9)	46	—	—	32.3 (3.5)	49	ns

* Statistical significance derived from a one-way analysis of variance (ns, no significant difference [$p > 0.05$]).

Table 2. Results of multiple-regression analyses^a for fruit set (percent of potential fruit set) in seven plant species relative to features of the habitat fragments in which they occurred.

Species	No. of sites	No. of flowers and/or plants	R ²	p	Main variables ^b
<i>Babiana ambigua</i>	9	54	0.98	<0.05	F, P, M
<i>Berkbeya armata</i>	9	104	0.20	ns ^c	—
<i>Cyanella lutea</i>	8	105	0.63	<0.05	M, P
<i>Gladiolus liliaceus</i>	6	96	0.46	ns	—
<i>Ornithogalum thyrsooides</i>	12	96	0.59	ns	—
<i>Pterygodium catholicum</i>	10	495	0.96	<0.05	F, M
<i>Trachyandra birsuta</i>	7	87	0.72	<0.05	M, F

^aData are from the best-fitting regression model for each species.

^bVariables tested were fragment size (F), perimeter (Pe), distance to "mainland" (M), nearest-neighbor distance (D), and pollinator diversity (P).

^cNo significant difference (ns; $p > 0.05$).

Pollinator Limitation

Based on our initial grouping of large, medium, and small fragments, statistically significant differences in fruit set were found only in populations of *P. catholicum* (greater in large fragments, $F_{1,7} = 6.29$, $p < 0.05$) and *B. ambigua* (greater in small fragments, $F_{2,6} = 6.38$, $p < 0.01$) (Table 1). Multiple-regression models, based on actual fragment size and incorporating other variables, showed significant regressions in four of the seven species tested (Table 2). Fragment size was a significant variable in two of the regressions (Table 2), with greater fruit set in large fragments for *P. catholicum* and the reverse for *B. ambigua*. Distance to the mainland influenced the regressions for four species (Table 2), with a consistent decline in fruit set in more isolated fragments. Pollinator diversity emerged as an additional significant variable for *B. ambigua*, with low fruit set associated with low pollinator diversity.

Results of hand-pollinated treatments for *G. liliaceus* and *O. thyrsooides* showed no increase in fruit set compared with naturally pollinated controls in fragments of any size (Table 3). Fruit set in these taxa was therefore not limited by a pollination deficit. In contrast, there was a substantial increase in fruit set when *P. catholicum* flowers were hand-pollinated (Table 3). Fruit set also increased when *B. ambigua* flowers were hand-pollinated. Many of the flowers and fruits were eaten by herbivores, however, so there were too few flowers to analyze statistically.

There were no significant differences (ANOVA, $p > 0.05$) in fruit production between hand-pollinated flowers of *G. liliaceus*, *O. thyrsooides*, and *P. catholicum* from different-sized fragments. Factors other than pollinator limitation that could have affected fruit production on different-sized fragments therefore appeared to be constant between different-sized fragments.

Germination and Reproductive Success

Germination success for *O. thyrsooides* seeds collected from different fragments was generally high (>80%), with most seeds germinating within 4 weeks of incubation. There was no statistically significant effect of fragment size, pollination treatment, or the interaction between these factors on germination success. Fragment size was not correlated with plant population size in *O. thyrsooides* (Spearman rank correlation coefficient = 0.02, $n = 36$), so population size was included as an independent variable. There was no significant difference in the number of fruits per flower in plants from different populations (Fig. 3), but number of seeds per fruit and percent germination varied significantly between population size classes (Fig. 3). As a result, overall reproductive output—number of seeds per plant \times proportion that germinated—was highest in large populations.

There was a significant negative correlation between fragment size and population size for *B. ambigua* (Spearman rank correlation coefficient = 0.939, $p < 0.01$, $n =$

Table 3. Comparison of fruit set (%) in hand-pollinated and control plants of three perennial species in large, medium-sized, and small fragments of renosterveld shrublands.

Species	Fragment size	Fruit set (SE)				p*
		control	n	hand pollinated	n	
<i>Gladiolus liliaceus</i>	small	89.4 (4.2)	36	87.6 (5.6)	27	ns
	large	96.7 (2.01)	15	93.1 (4.02)	17	ns
<i>Ornithogalum thyrsooides</i>	small	84.2 (7.8)	20	94.1 (2.3)	20	ns
	medium	93.5 (8.5)	20	97.4 (3.6)	20	ns
	large	95.2 (1.5)	20	95.0 (1.1)	20	ns
<i>Pterygodium catholicum</i>	small	0	213	53.2 (7.3)	111	<0.01
	large	14.3 (10.4)	240	84.2 (6.9)	65	<0.01

*Statistical differences were determined with a one-way analysis of variance with arcsin-transformed values (ns, not significant).

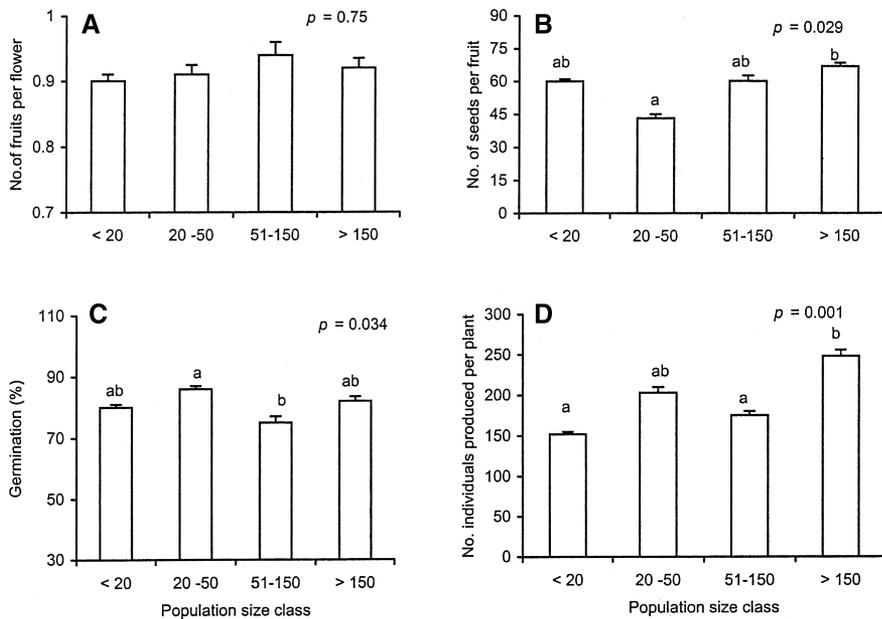


Figure 3. Mean (1 SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success, and (d) individuals produced per plant for *Ornithogalum thyrsoides* in four population size classes. Significance levels for one-way analysis of variance and back-transformed means are given. Columns that share the same letter do not differ significantly from one another (Tukey multiple-range test).

19), in that smaller fragments had larger plant populations than large fragments. Germination success for *B. ambigua* seeds collected from large fragments (small populations; 96.3%) was significantly greater (Fig. 4) than that of seeds from either medium (4.3%) or small (36%) fragments (large populations). However, plants from small fragments produced many more seeds than those from medium or large fragments ($p < 0.01$), resulting in a significantly higher reproductive output per plant from small fragments (16.8) than from medium (0.5) or large (5.1) fragments (Fig. 4).

Fruit set in large populations of *B. ambigua* (i.e., on small fragments) was about twice that of small populations (Fig. 4), and seed set increased substantially in

large populations (Fig. 4). However, germination success was significantly higher in seeds from small populations (large fragments). Despite lower germination success, there was an overall increase in reproductive output for plants from large populations (small fragments) (Fig. 4).

Discussion

Our results highlight the complex nature of plant reproduction in fragmented landscapes (Aizen & Feinsinger 1994a) and the difficulties associated with predicting the outcome of fragmentation on plant extinctions. Contrary to our expectations, the overall species richness

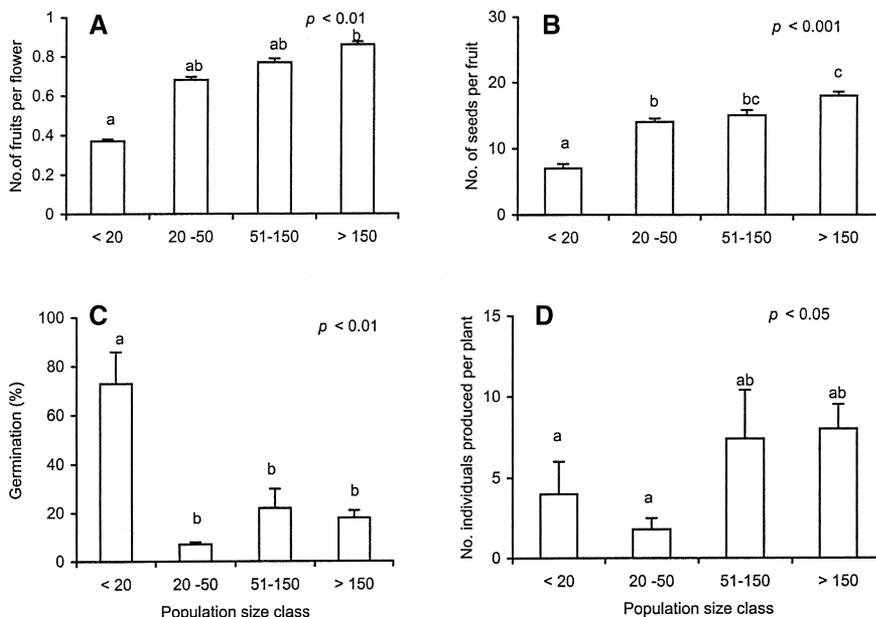


Figure 4. Mean (1 SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success, and (d) individuals produced per plant for *Babiana ambigua* in four population size classes. Significance levels for one-way analysis of variance and back-transformed means are given. Columns that share the same letter do not differ significantly from one another (Tukey multiple-range test).

and composition of pollinators did not vary substantially between fragments of different sizes, even though small fragments were exposed to insecticide drift from surrounding croplands. The only consistent trend was a decrease in abundance with increasing distance from large fragments, indicating that large fragments could act as a source of pollinators. Otherwise, pollinator species showed species-specific responses to fragment size, extent of vegetation cover, and degree of rockiness.

In contrast to the results of Spears (1987), Menges (1991), and Jennersten (1988), who all found that plant reproductive success on small islands was lower than in large areas, our results were varied. Four perennial plant species showed no discernible change in fruit or seed set across a range of fragment sizes, two species produced fewer fruits or seeds on small fragments, and one species produced fewer fruits on large fragments. Reproductive success appeared to be influenced by factors such as vegetation cover, the availability of pollinators, and plant population size. These results require further interpretation to determine how they relate to our understanding of pollination and plant reproduction in fragmented systems and to clarify their consequences for the conservation of renosterveld shrublands.

Pollinators and Habitat Fragmentation

Insect pollinators were more sensitive to habitat characteristics—percent vegetation cover, percent grass, and rockiness—than to fragment size. Even small fragments of <1 ha contained a high diversity of insect pollinators. Monkey beetles, which have been identified as important pollinators of renosterveld plant species (Picker & Midgley 1996; Goldblatt et al. 1998; Steiner 1998), appeared particularly sensitive to changes in habitat. Results of studies on invertebrates in other fragmented systems suggest that vagrant species increase the species diversity of small fragments (Mader 1981; Webb 1989). Vagrant species, moving from the matrix into small fragments, did not seem to alter the diversity on small renosterveld fragments, because the majority of pollinator species were recorded from both large and small fragments (Fig. 2).

Vegetation cover has been identified as a determinant of insect species diversity in fragmented landscapes (Webb 1989). Despite our efforts to choose fragments with similar aspect, slope, vegetation, and soils, there were discernible differences in overall vegetation cover, degree of dominance by few shrub species (mainly *Elytropappus rhinocerotis*), and density of flowering geophytes. Shrubs were often dominant in sampling sites on large fragments, whereas smaller fragments were more heterogeneous. Such differences would almost certainly influence the microclimate (Saunders et al. 1991) and could also be linked to changes in soil structure. Both factors would be expected to influence the diversity and abundance of insects that nest or live

in the soil, such as monkey beetles and ground-nesting bees (Gess & Gess 1993). Similarly, changes in vegetation cover and the ratio of shrubs to grasses would influence the availability of nesting sites for twig-nesting bees and wasps (Gess & Gess 1993; Cane 2001). The dominant shrubs on large fragments (e.g., *E. rhinocerotis*) have woody stems that appear to be a poor nesting resource for bees. Plants such as *Berkheya rigida*, with pithy stems suitable for bee nests (Gess & Gess 1993), flourished in disturbed sites (usually smaller fragments). As a result, nest sites may occur at high densities in smaller fragments and therefore compensate for differences in fragment size.

A further factor that may have influenced pollinator diversity and abundance was the availability of floral resources. High densities of flowering geophytes have been recorded in small remnants of renosterveld (Kemper 1997), especially areas with relatively low shrub cover. Resources for pollinators do not decline linearly with decreasing fragment size, and even quite small fragments (<1 ha) can maintain or attract a diversity of insect pollinators.

Habitat Fragmentation and Reproductive Failure

Different plant taxa and different pollination systems are expected to vary in their response to habitat fragmentation (Aizen & Feinsinger 1994a, 1994b; Bronstein 1995). Our results strongly support this prediction. Nevertheless, a crucial question for plant conservation is whether the apparent complexity of possible outcomes can be simplified by identifying groups of plants and pollinators that will respond to fragmentation in similar ways (i.e., response types). To address this question, we specifically selected a range of plants with different pollination systems.

Bronstein (1995) proposes that the most important attributes for determining the effect of fragmentation on pollination are the timing, duration, and intensity of flowering in plants, simplified as synchronous or asynchronous flowering, and the search behaviors and diet breadth of their pollinators, simplified as generalized or specialized pollinators. On this basis, Bronstein (1995) identified four response groups (pollinator landscapes; sensu Bronstein 1995) and a fifth category of migratory pollinators. Bronstein's (1995) classification provides a useful context for interpreting our results.

The spring-flowering geophytes we studied have a short and highly synchronized flowering season, but the pollinators varied from specialist oil-collecting bees in the genus *Rediviva* (for *P. catholicum*) to generalist beetles and bees (e.g., for *O. thyrsoides*). This variation provided a range possible of outcomes.

Bronstein (1995) postulates that there would be a high failure rate among pollination systems involving specialized pollinators and synchronously flowering plants. Our results tend to support this argument. The

oil-producing orchid, *P. catholicum*, produced no fruits on small or medium-sized fragments. The abundance of *Rediviva* species, such as those associated with *P. catholicum*, varies sharply from year to year (K. Steiner, personal communication), and it is possible that bees reach smaller fragments in years of greater abundance. Nevertheless, the absence of pollination on small fragments in some years decreases the plant's chances of survival on small fragments relative to large ones.

Similarly, fruit set in *C. lutea*, which is buzz-pollinated, was significantly reduced in fragments that were farther from large mainland areas. Although several bee species may be involved in buzz pollination, the interaction represents a relatively specialized pollination system. As such, the decline in fruit set of *C. lutea* in response to increasing isolation supports Bronstein's prediction.

The combination of generalized pollinators with synchronously flowering plants is expected to be common in nature (Bronstein 1995), and most of the plants we studied fell into this group of pollinator interactions. Despite the apparent similarity of these pollination systems, our results highlight some of the variation that exists in the way generalized pollinators and their forage plants respond to habitat fragmentation. Three plant species with generalized pollinators, *B. armata*, *G. liliaceus*, and *O. thyrsoides*, showed no discernible change in fruit or seed set in response to fragmentation. In contrast, *T. hirsuta* which was regularly visited by bees, flies, and beetles, produced significantly fewer fruits on small fragments than on large ones. This means seed set may be pollinator-limited even in plants that are pollinated by generalized pollinators. Schemske and Horvitz (1984) showed that, where plants are dependent on generalized pollinators, there may be relatively few effective pollinators among the large number of insects that actually visit flowers. Effective pollinators may even be absent (Horvitz & Schemske 1990). The differences in insect abundance that we recorded on different fragments could have influenced fruit set in plants that depended on generalized pollinators.

The nature of generalized pollination interactions may also influence the outcome of fragmentation. For example, many potential pollinators visited *T. hirsuta*, whereas *G. liliaceus* was pollinated only by a generalist noctuid moth, *Cucullia extricata*. Under these circumstances, we expected *G. liliaceus* to be more vulnerable to pollinator limitation than *T. hirsuta*—the opposite of our results—because the distribution and abundance of *C. extricata* would have a substantial effect on pollination of *G. liliaceus*. But *G. liliaceus* probably did not experience pollinator limitation in small fragments because of the apparently robust habitat requirements of its pollinator. Like many noctuids, *C. extricata* has a broad larval host range (Pinhey 1975), so it may perceive large sections of the landscape matrix to be suitable habitat and therefore may be relatively unaffected by habitat frag-

mentation. Our results suggest that the overall habitat requirements of pollinators may have a greater effect on pollination than simply the floral specialization of the pollinator (Cane 2001).

Another factor that influenced plant reproduction was plant population size, which was not always correlated with fragment size. The reproductive output of both *O. thyrsoides* and *B. ambigua* was greater in large populations than in small ones, irrespective of fragment size. Fruit set was generally greater in large populations, where flowers occurred at higher densities. Such changes in plant populations would be expected to influence pollinator visitation rates (Handel 1983), pollinator fidelity (Sowig 1989), and rates of outcrossing (Handel 1983). It is not clear whether observed differences in fruit set would be consistent from year to year, because high reproductive output in a population may result in flowering depression the following year (Johnson 1992) due to depleted resources (Zimmerman & Aide 1989).

Seed germination in *B. ambigua* was significantly greater in small populations associated with large habitat fragments. The variation in percent germination may reflect differences in pollen quality, with scattered flowers on large fragments receiving more out-crossed pollen. Alternatively, it may be a consequence of greater pesticide and herbicide use on small and medium-sized fragments resulting in an overall lower fitness of seeds in these sites.

Plant breeding systems may compensate for the absence of pollinators. *Ornithogalum thyrsoides* was capable of autogamy and selfing. Seeds arising from autogamous fertilization still had a germination success of 78%, only 10% lower than the germination success recorded for seeds from outcrossed flowers in field experiments. The capacity for selfing and autogamy is an important factor that distinguishes *O. thyrsoides* from other species with generalist pollinators such as *B. ambigua* and *T. hirsuta*, which appeared to be self-inferile. Ultimately, plant success in habitat fragments will also be influenced by other factors such as seed dispersal, seedling establishment, and the longevity of individual plants (Aizen & Feinsinger 1994b; Bond 1994).

Conservation in Renoster Shrublands

Despite the persistence of many pollinator species on small fragments, our study shows that perennial plants are more vulnerable to pollination failure on small, isolated fragments than on large or well connected ones. In several cases, fruit set was a function of distance to large patches, suggesting that large patches are a source of pollinators. This may be because large patches provide a critical threshold of resources for pollinators.

Where there was a decline in pollinators or fruit set on large fragments (e.g., *B. ambigua*), this appeared to be due to a lack of habitat heterogeneity resulting from the dominance of a few shrub species. Our data therefore in-

dicating that larger fragments need to be managed in a way that increases habitat heterogeneity, reduces the density of shrubs, and promotes flowering by the high diversity of spring-flowering geophytes.

Small fragments may contain important populations of rare or threatened plant species, and it is important to ensure that nearby large fragments are retained as potential sources of pollinators. At present, we do not know whether the establishment of corridors between large and small fragments is needed to enable pollinators to move from source areas to small fragments.

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