

COLLAPSE OF A POLLINATION WEB IN SMALL CONSERVATION AREAS

ANTON PAUW¹

Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602 South Africa

Abstract. A suspected global decline in pollinators has heightened interest in their ecological significance. In a worst-case scenario, the decline of generalist pollinators is predicted to trigger cascades of linked declines among the multiple specialist plant species to which they are linked, but this has not been documented. I studied a portion of a pollination web involving a generalist pollinator, the oil-collecting bee *Rediviva peringueyi*, and a community of oil-secreting plants. Across 27 established conservation areas located in the Cape Floral Region, I found substantial variation in the bees' occurrence in relation to soil type and the successional stage of the vegetation. Anthropogenic declines were detectable against this background of naturally occurring variation: *R. peringueyi* was absent from small conservation areas (<385 ha) in an urban matrix. In the absence of the bee, seed set failed in six specialist plant species that are pollinated only by *R. peringueyi* but remained high in a pollination generalist, which had replacement pollinators. The findings are consistent with theoretical predictions of the importance of generalist pollinators in maintaining the structure of pollination webs.

Key words: cascade effects; conservation; fire ecology; habitat fragmentation; mutualism disruption; Orchidaceae; pollen limitation; pollination web; *Pterogodium catholicum*; *Rediviva peringueyi*; South Africa.

INTRODUCTION

A suspected global decline in pollination, the “pollination crisis,” has heightened interest in the ecological significance of pollinators (Buchmann and Nabhan 1996, Allen-Wardell et al. 1998, Kearns et al. 1998, Steffan-Dewenter and Tscharrntke 2002, Biesmeijer et al. 2006). In a worst-case scenario, generalist pollinators are predicted to be sensitive to human-caused disruption, and their early loss will trigger a cascade of linked declines among the multiple plant species that they pollinate (Gilbert 1978, Cox 1983), but this has not been documented. In fact, a recent review found that there was insufficient evidence to support the popular idea of a “pollination crisis” (Ghazoul 2005). The review found, first, that there was a lack of evidence for an anthropogenic decline in pollination by wild pollinators at a regional scale, and second, questioned the ecological significance of pollinators.

Studies of human-caused declines in pollination have most often focused on the effects of habitat fragmentation, because this is perceived to be the major threat to wild pollinators (Kearns et al. 1998, Aguilar et al. 2006). Although some research hints that a large-scale approach is necessary (Steffan-Dewenter et al. 2002), most studies have been confined to relatively small spatial scales (e.g., Jennersten 1988, Aizen and Feinsinger 1994, Cunningham 2000, Lindberg and Olesen 2001, Donald-

son et al. 2002, Lennartsson 2002), leaving the question of whether pollination is sensitive to habitat fragmentation at the scale of established conservation areas unanswered.

Generalist pollinators are the center of interest. They are linked to multiple plant species and therefore their loss has the potential to precipitate cascades of linked declines leading to the acceleration of biodiversity loss (Gilbert 1978, Cox et al. 1991). Recent insights into the structure of pollination webs emphasize the possible significance of generalist pollinators. Pollination webs are asymmetrically specialized, so that plants linked to generalist pollinators tend to be specialists (Bascompte et al. 2003, 2006, Vazquez and Aizen 2004). Thus, the loss of a generalist pollinator will primarily affect specialist plant species which, by definition, are vulnerable to this loss because they have no replacement pollinators (Rathcke and Jules 1993, Aizen and Feinsinger 1994, Bond 1994). However, while the web might be sensitive to losing generalist pollinators, these losses are predicted to be unlikely because the broad floral preferences of generalist pollinators buffer them against extinction (Ashworth et al. 2004, Bascompte et al. 2006, Fortuna and Bascompte 2006, Pemberton and Wheeler 2006).

In contrast with recent theoretical developments, empirical studies of pollination decline have typically considered effects on single plant species (Aguilar et al. 2006) or a selection of heterogeneously pollinated plant species (e.g., Aizen and Feinsinger 1994), and have not tested the prediction that the loss of a generalist pollinator species will have multiple detrimental effects

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¹ E-mail: apauw@sun.ac.za

among linked specialists in the pollination web. In order to test this contention, I studied a portion of a pollination web involving an oil-collecting bee species, *Rediviva peringueyi* Friese (Hymenoptera: Melittidae), and a community of 21 oil-secreting plant species that are pollinated by the bee (Whitehead and Steiner 2001, Pauw 2005, 2006). The community is asymmetrically specialized, such that most of the plant species are specialist orchids, pollinated only by this single bee species, while the bee is a generalist that pollinates all the plant species in the oil-secreting plant community. The exception among the study plants is *Hemimeris racemosa* (Houtt.) Merrill, a generalist oil-secreting member of the Scrophulariaceae that is pollinated by several species of oil-collecting bees, including *R. peringueyi*.

The pollination web considered here is simple relative to complex webs that include extreme generalists. Nevertheless, *R. peringueyi* exemplifies the important features of a generalist pollinator, namely, that it is linked to multiple specialists and its loss therefore has the potential to trigger multiple declines. In its degree of generalization, *R. peringueyi* is comparable with the flying foxes and hermit hummingbirds that led Gilbert (1978) and Cox et al. (1991) to formulate their hypotheses about the important role of generalist pollinators in the interaction web.

The *R. peringueyi* pollination community is centered in the west coast lowlands of the Cape Floral Region of South Africa, a global hotspot of biodiversity (Goldblatt and Manning 2002). Over most of the lowlands, natural habitats have been reduced to small remnants by agricultural and urban expansion (McDowell and Moll 1992, Hejnis et al. 1999, Maze and Rebelo 1999), but conservation areas of varying size have been established, or are being planned, to conserve the endemic lowland flora (Hejnis et al. 1999, von Hase et al. 2004). I selected 27 established conservation areas and asked: "Are these large enough to adequately conserve *R. peringueyi*, and if not, does their loss trigger a cascade of declines in seed set among the community of specialized oil-secreting plants species to which they are linked?"

The bee is difficult to observe because it is uncommon, and visits to oil-secreting plants are infrequent. I focus instead on *Pterygodium catholicum* (L.) Sw., the most common orchid in the community, and record patterns of variation in its seed capsule set. I make the link back to the bee by establishing that variation in the activity of this pollinator determines variation in capsule set, and thus that capsule set in this species can be used as a proxy of the bees' activity. I then examine the impact of habitat fragmentation on the pollination system by analyzing variation in capsule set in *P. catholicum* in relation to the size of conservation areas and the type of anthropogenic matrix in which the conservation areas are located. Because the study area is large, the effect of these anthropogenic factors is considered in the context of natural variability caused by soil type differences across the region and differences in postfire successional

stage. Finally, I look for correlated patterns of capsule set among the members of the *R. peringueyi* pollination community with the aim of determining whether the loss of a generalist pollinator can trigger a cascade of declines in seed set among multiple, linked pollination specialists. The pollination generalist, *H. racemosa*, which is also linked into the *R. peringueyi* pollination web, is predicted to be little affected.

METHODS

Study species

The principal study species, *P. catholicum* (see Plate 1) is the most common orchid in the Cape flora. Plants flower profusely in the first few years after fire but produce only leaves in late-successional vegetation. Inflorescences are ~15 cm in height and have a median of three flowers (mean \pm SE = 3.67 ± 1.67 flowers; range = 1–12 flowers, $n = 2791$). Individual flowers remain open for four weeks if not pollinated. The flowers secrete oil as a reward, which is collected by females of the solitary oil-collecting bee *R. peringueyi* (Pauw 2006). The oil is probably used to provision subterranean nest cells. The pollen packets (pollinaria) of *P. catholicum* become attached to the middle legs of the bee while it collects oil from the flower with its modified front legs. After pollination, the flower produces a capsule filled with microscopic seeds. In addition to sexual reproduction via seeds, extensive vegetative reproduction occurs through the formation of daughter tubers on the ends of stolonoid roots (Pauw 2004).

Six additional members of the *R. peringueyi* pollination community were included in the assessment of community-wide impacts of the loss of *R. peringueyi*. These include the orchids *Pterygodium alatum* (Thunb.) Sw., *P. caffrum* (L.) Sw., *P. volucris* (L.f.) Sw., *Corycium orobanchoides* (L.f.) Sw., and *Disperis villosa* (L.f.) Sw., which are specialized for pollination by *R. peringueyi* and possess a set of convergent floral features (Pauw 2006); and *Hemimeris racemosa* (Scrophulariaceae), which, within the study areas, is pollinated by four *Rediviva* species (Pauw 2005). Only the inversostylous, outcrossing morph of this species is included in this study. Insufficient data could be obtained for the remaining plant species in the community because they are very rare or patchily distributed.

Self-compatibility occurs in *P. catholicum*, and probably in the other orchid species as well. Even so, all the orchid species included in this study are incapable of autogamy (Pauw 2006). In contrast, *H. racemosa* has a limited capacity for autogamy. Pollinator exclusion significantly reduced capsule set in this species, but pollinator-excluded plants still set up to 20% of their capsules (Pauw 2005).

Study sites

I selected 27 areas of natural vegetation within a 12 500 km² study area located in the west coast lowlands of South Africa (Fig. 1) (Appendix A). Most of these

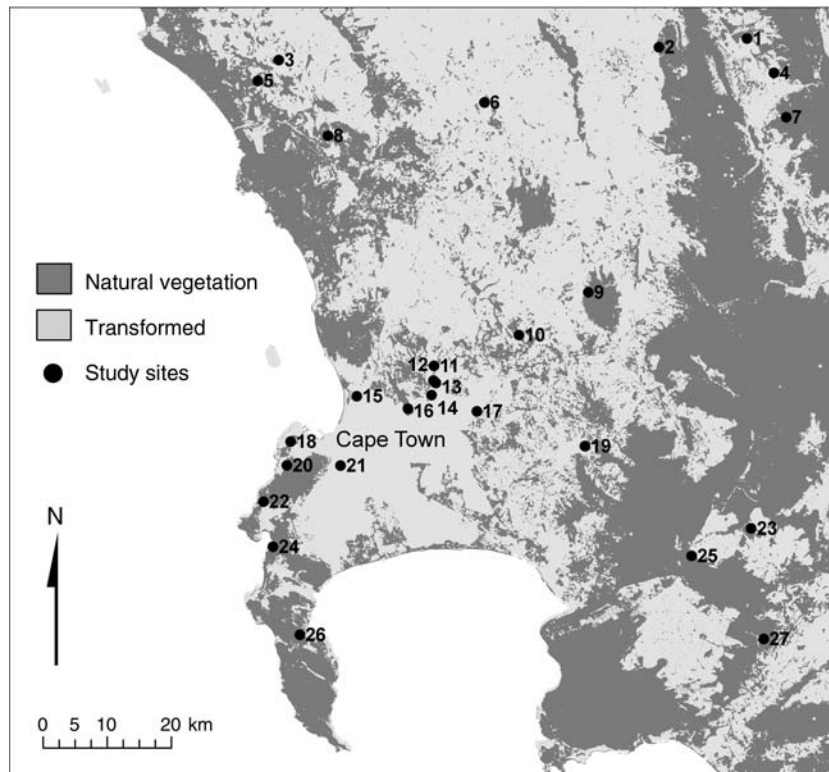


FIG. 1. Location of study sites in the Cape Floral Region of South Africa where pollination rate by the oil-collecting bee *R. peringueyi* was monitored over a four-year period. Once continuous, natural vegetation has been reduced to small fragments by agricultural and urban expansion, particularly on the coastal plateau where the city of Cape Town is located. Study site numbers link with site data in Appendix A.

were proclaimed conservation areas aimed at the conservation of the endemic lowland flora. The climate is Mediterranean, and the vegetation is a fine-leaved, fire-prone shrubland with interfire periods of ~12 years (Low and Rebelo 1996). There is a long history of intensive land use; thus, conservation areas have been isolated from each other by transformed areas for between 50 and 150 years (McDowell and Moll 1992). The study area covered between 80% and 50% of the distribution range of the plants species, and 90% of the known range of the pollinator (Whitehead and Steiner 2001).

Dependent variable: capsule set

Capsule set is the main dependent variable in this study. I recorded capsule set in the orchids by marking flowering plants (September) with adhesive jewelry tags and returning after flowering (October to November) to determine the proportion of flowers that had produced seed capsules. Long after flowering, the withered flowers remain attached to the inflorescence, whether or not they produce seed capsules. Successful seed set is indicated by a swollen ovary (a capsule), which dehisces along longitudinal slits. Aborted ovaries are shriveled and twisted and contain masses of unfilled seeds still attached to the three parietal placentas. Swollen and

dehiscent capsules were opened in the field and checked under 10× magnification for the presence of filled seeds. The seed coat is translucent, allowing easy distinction between filled and unfilled seeds. Filled seeds are spindle shaped, swollen in the middle, and have dark brown contents. Unfilled seeds are not swollen in the middle, and have light-colored contents. I recorded capsule set, rather than seed set, because seeds are minute and numerous and are released from the capsules soon after maturation. In the *Disperis* and *Pterygodium* species, all flowers on sample inflorescences were checked. In *C. orobanchoides*, underdeveloped, apical flowers that are easily identified by their small size even after flowering were excluded. Capsule set in *H. racemosa* was determined in a similar way. In this species undeveloped capsules are 1/10th the size of developed capsules.

For *P. catholicum*, the median number of sample years at each of 27 conservation areas was 2 (range 1–4). The median sample size was 122 flowers (range, 13–799 flowers). In total, capsule production was recorded for 10 101 *P. catholicum* flowers on 2791 plants (Appendix A).

Proximate determinants of capsule set in P. catholicum

A close link between pollination rate and seed set is necessary if pollinator loss is to have an ecological effect.

In addition, a close relationship between pollination and capsule set would allow the use of capsule set in *P. catholicum* as an easily determinable proxy for pollination rate by *R. peringueyi*. However, variability in the availability of resources, such as nutrients and water, is often an important source of variance in capsule set and may preclude the use of capsule set as a measure of pollination rate. To test whether capsule set is a good predictor of pollination rate, I quantified pollination rate and related it to capsule set data obtained during the same sample year. Pollination rate was quantified in two ways.

1) Field-collected orchid flowers were checked to determine whether the pollinaria had been removed and whether there were pollen massulae (sections of pollinaria) adhering to the stigma. Wilted inflorescences were collected at the end of the flowering season and preserved in 70% ethanol before microscopic dissection (40 \times magnification). I recorded the presence or absence, rather than number, of massulae on the stigma since one massula is sufficient to fertilize all the ovules (S. D. Johnson, *personal communication*). Empty, but undamaged, pollinarium sacs indicated pollinarium removal by a pollinator. Occasional pollinaria removed by pollen-feeding insects can be identified (and excluded), because herbivorous insects cause damage to the membranous pollinarium sac and typically eat the pollen, but not the viscidium (pollinarium attachment disc) or caudicle (arm). Pollination rates were determined at 15 study sites. Median sample size was 115 flowers (range, 35–241) and 27 plants (range, 11–59). In total, pollination rates were determined for 1795 flowers on 436 plants.

2) Censuses of pollinator visitation rate were conducted at 11 of the sites by observing $\sim 5\text{-m}^2$ patches of *H. racemosa* plants for two 15-minute intervals from a distance of 2 m. This member of the Scrophulariaceae grows in dense patches where many flowers can be observed simultaneously (Pauw 2005). Four *Rediviva* species visited the flowers of *H. racemosa* at the study sites. However, it was possible to distinguish *R. peringueyi* from other *Rediviva* species with reasonable certainty on the basis of its larger size. Visitation rate observations were restricted to warm ($>20^\circ\text{C}$), windless hours between 10:30 and 15:30 hours. Visitation rate was calculated as visits per flower per hour.

The correlative analysis of the relationship between pollination rate and capsule set in *P. catholicum* was experimentally tested in two ways: (1) At Rondebosch Common, a site with low capsule set, I supplemented natural pollination by hand-pollinating all the flowers on 21 plants. Pollinaria were collected using a bent dissecting needle and dabbed onto the stigma of another plant, which could be accessed only by freeing the tip of the lip appendage from the dorsal sepal. Capsule set in experimental plants was compared with a further 82 control plants that received only natural pollination. (2) On the Darling Hills, a site with high capsule set, I excluded pollinators from 16 plants with fine gauze bags

stretched over wire frames. Capsule set in experimental plants was compared with a further 66 control plants left open to receive natural pollination.

Ultimate determinants of capsule set in P. catholicum

Generalized linear models were used to explore the relationship between environmental variables and capsule set in *P. catholicum*. The aim was to establish whether the *R. peringueyi* pollination system was sensitive to habitat fragmentation at the scale of established conservation areas. However, in order to detect an anthropogenic effect it was important to account for naturally occurring spatial and temporal variability in capsule set. The explanatory variables included the following anthropogenic as well as natural factors.

1. *Size of conservation area.*—The size of the 27 remnants of natural vegetation (conservation areas) was determined from a fine-scale digital map of natural remnants using geographic information system software (Arcview 3.2 and ArcInfo 8.2, Environmental Systems Research Institute, Redlands, California, USA). The map was produced from LANDSAT7 imagery, ground-truthed and manually refined as described in Lloyd et al. (1999) and von Hase et al. (2004). The boundaries of reserves were drawn to include any areas of untransformed land that were continuous with the formally proclaimed conservation area. Large conservation areas ($>100\,000$ ha) could not be objectively delimited, and in some cases linked through to vast areas of untransformed land in the center of South Africa (Fig. 1). Because quantification was problematic, conservation areas were classified. Large conservation areas ranged from 2579 ha to $\sim 150\,000$ ha (median = 15 805 ha, $n = 13$); small conservation areas range from 4 ha to 609 ha (median = 30 ha, $n = 14$) (Appendix A). Reserve size [large; small] was a categorical fixed factor.

2. *Matrix in which the reserve is located.*—Matrix type is likely to determine permeability to pollinator movement and hence the degree of isolation of conservation areas. Conservation areas were located either in a rural matrix, consisting mostly of plowed fields used for crop or livestock production, or in an urban matrix within the Cape Town Metropolitan area. Matrix type [urban; rural] was a categorical fixed factor.

3. *Soil type.*—In a simplified view, the Cape consists of a mosaic of two fundamentally different soil types: coarse-grained, sandy soils, poor in essential plant nutrients, and finer-grained clay soils richer in nutrients (Goldblatt and Manning 2002). The vegetation changes across this boundary from fynbos (sandy soils) to renosterveld (clay soils) (Low and Rebelo 1996). Soil type also correlates with altitude, rainfall, and temperature. Soil type was included in the analysis because of these considerations, as well as the observation that ground-nesting bees are sensitive to soil texture (Gess and Gess 1993, Vinson et al. 1993, Westrich 1996, Cane et al. 2006). Soil type [clay; sand] was a categorical fixed

factor. Sandy conservation areas in a rural matrix tended to be large, because agriculture has made limited inroads into these infertile substrates.

4. *Successional stage of the vegetation.*—The number of years since fire occurred was included on the basis of the observation that the density of oil resources declines sharply as succession proceeds. Flowering in the *R. peringueyi* pollination community is strongly fire stimulated, while in the annual *H. racemosa*, germination from a soil-stored seed bank is triggered by fire. For recently burned sites the time since the last fire was known; for sites that were not burned recently, the time since the last fire was determined from the age of shrubs. The postburn age of the vegetation was a continuous fixed variable ranging in value from 1 to 13 (median 3).

Plants from one conservation area were pooled, so that the total number of flowers sampled at a site was the number of “trials,” and the number of capsules produced was the number of “successes.” As a first step, generalized linear models (GLM) with quasi-binomial error structure were fitted in the statistical software R, version 1.6.0 (Venables and Ripley 2002). Starting from the full model, which included all possible interaction terms between the four explanatory variables, the minimal adequate GLM was obtained by sequential removal of nonsignificant model terms (analysis of deviance, *F* tests, $P > 0.05$). The selected minimum adequate GLM contained all main effects of the four variables plus the interaction between matrix and size. The minimum adequate GLM included pseudoreplication because some sites were sampled repeatedly in successive years. At the final stage of analysis, pseudoreplication was avoided by including site as a random effect (nested within successional stage) in a generalized linear mixed model (GLMM) (function `glmmPQL`; penalized quasi likelihood approach; random effects of site on intercept and slope).

Multiple linked effects

To determine whether the loss of a generalist pollinator can trigger a cascade of declines in seed set among linked specialists, I looked for correlated patterns of capsule set among the members of the *R. peringueyi* pollination community. For six species (five specialist orchids and one generalist member of the Scrophulariaceae), there were sufficient sites of co-occurrence to allow capsule set variation across sites to be correlated with capsule set in *P. catholicum*. Positive correlation across sites would be consistent with the interpretation of multiple, linked declines. Each site was sampled once only. The average capsule set was determined for each species and related to the average capsule set in *P. catholicum* at the same site. (See the sampling scheme for *P. catholicum* in *Dependent variable: capsule set* and following sections.) Data were arcsine transformed to normalize the error distribution before analysis with Pearson correlation. An alternative approach, not taken here, would have been to include

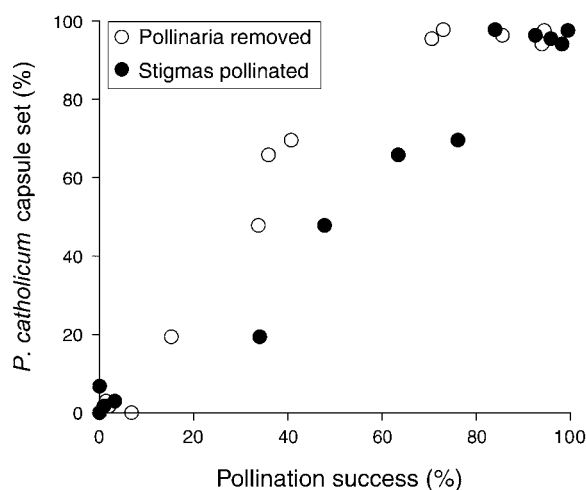


FIG. 2. Correlation across 15 sites between the percentage of *P. catholicum* flowers producing seed capsules and two measures of pollination success: the percentage of pollinaria removed by pollinators (open circles; Pearson's $r = 0.97$, $P < 0.0001$, $N = 15$) and the percentage of stigmas with adhered pollen (filled circles; Pearson's $r = 0.99$, $P < 0.0001$, $N = 15$).

data from these additional species in the GLMM described earlier. A correlative approach was chosen instead, because it more clearly illustrates matched responses among the members of the oil-secreting community. The median (range) of the number of flowers sampled at each site was: *Pterygodium alatum* 255 (58–738 flowers); *P. caffrum* 198 (58–445 flowers); *P. volucris* 126 (37–535 flowers); *Corycium orobanchoides* 215 (19–1712 flowers); *Disperis villosa* 6 (6–23 flowers); and *Hemimeris racemosa* 870 (70–2885 flowers). The number of sites sampled appears in Fig. 5. For this portion of the study, capsule set was determined for a total of 27 382 flowers.

RESULTS

Proximate determinants of variation in capsule set in *P. catholicum*

Capsule set in *P. catholicum* varied among conservation areas from 0% to 98% (median 18%, mean 38%) (Appendix A). There are three common proximate sources of variation in seed set in plants: (1) variation in the availability of growth resources, (2) variation in the availability of genetic resources, and (3) variation in pollination rate (Wilcock and Neiland 2002). In the case of *P. catholicum* correlative and experimental data lend support to the latter explanation.

Variation in two measures of pollination rate (the percentage of stigmas that have received pollen, and the percentage of pollinaria that have been removed) explained almost all of the observed variation in capsule set, suggesting that factors other than pollination played a minor role (Fig. 2). The existence of a causal relationship between pollination and capsule set was confirmed by experimentation. Supplementation of

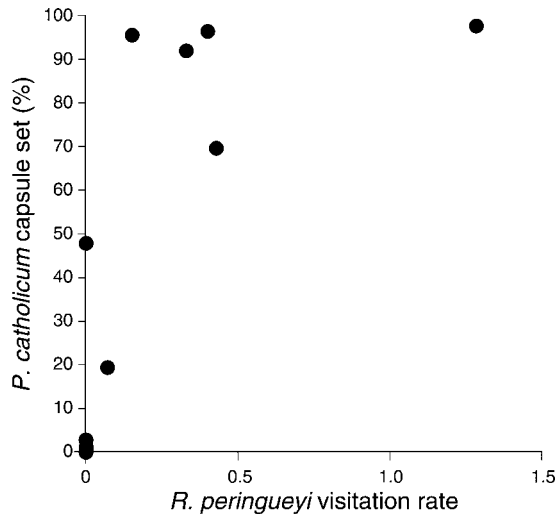


FIG. 3. Relationship between capsule set in *P. catholicum* and visitation rate (visits per flower per hour) by the oil-collecting bee *R. peringueyi*. Visitation rate was determined at the flowers of *H. racemosa*, an abundant, sympatric, oil-secreting host plant of *R. peringueyi* (Spearman's $r = 0.86$, $N = 11$, $P = 0.0007$). The data are consistent with the interpretation that the failure of capsule set indicates the absence of the bee.

natural pollination with hand pollination increased capsule set at a sandy site with low pollination rate from 0% to $78\% \pm 7\%$ (mean \pm SE), so capsule set failure was not due to a lack of growth resources (e.g., water and nutrients). Conversely, at a site with high pollination rate, the exclusion of pollinators with gauze bags reduced capsule production from $98\% \pm 1\%$ to 0%, indicating the role of pollinators in ensuring capsule set. Low pollination rates could not be attributed to a lack of genetic resources. Locally available pollen was used in the pollen supplementation experiment, suggesting that sufficiently good-quality pollen existed locally. In addition, the relationship between pollination and capsule set was not modified by herbivores. Very little evidence of herbivory or seed predation was observed. Lastly, the role of *R. peringueyi*, in particular, in determining capsule set is evident from pollinator censuses. At sites where *R. peringueyi* was absent, capsule set was low; where *R. peringueyi* occurred, capsule set was high (Fig. 3).

In summary, capsule set in *P. catholicum* can be used as a proxy for the pollination activity of *R. peringueyi*. Capsule set fails due to low levels of pollination by *R. peringueyi*. High levels of capsule set indicate high levels of pollination by this oil-collecting bee.

Ultimate determinants of capsule set in *P. catholicum*

Two sources of natural variability in the landscape significantly affected capsule set (Table 1). These were soil type [clay; sand], and the successional stage of the vegetation [years since fire, range 1–13]. Capsule set decreased with increasing postfire age of the vegetation, and was lower on sandy than on clay soils (Table 1, Fig. 4).

Two anthropogenic factors, namely the size of the conservation area [large; small] and the matrix in which it is located [urban; rural] did not have a significant effect on capsule set when considered separately, but the interaction between these two factors did have a significant effect (Table 1). Capsule set was significantly lower in small conservation areas if these were located in an urban matrix (Fig. 4).

Multiple, linked declines

Variation across sites in capsule set in *P. catholicum* correlated with variation in capsule set in the pollination specialists *P. alatum*, *P. caffrum*, *P. volucris*, *C. orobanchoides*, and *D. villosa*, indicating that variation in the abundance of their shared pollinator was having multiple, linked effects (Fig. 5). Most importantly, reproductive failure in *P. catholicum* in some conservation areas was matched by reproductive failure in the other five specialist species. Capsule set in the pollination generalist *H. racemosa* (Scrophulariaceae) did not correlate with capsule set in *P. catholicum*. In conservation areas where capsule set in *P. catholicum* was zero, *H. racemosa* was observed to be pollinated by smaller species of *Rediviva* (*R. bicava*, *R. intermixta*, and *R. parva*).

DISCUSSION

Some proclaimed conservation areas appear to be too small to sustain a population of a generalist pollinator, the oil-collecting bee *Rediviva peringueyi*. Its loss has collapsed a portion of a pollination web, resulting in community-wide failure of seed production among the

TABLE 1. Significance tests for the effect of reserve characteristics on capsule set in *Pterygodium catholicum* by means of a generalized linear mixed model.

Explanatory variable†	Value‡	SE	df	t	P
Intercept	1.93	0.46	32	4.24	0.0002
Soil [<u>sand</u> ; clay]	−3.72	1.00	22	−3.71	0.0012
Years since fire	−0.21	0.08	32	−2.50	0.0176
Matrix [<u>urban</u> ; rural]	−0.24	0.77	22	−0.31	0.7569
Size [<u>small</u> ; large]	−0.73	0.59	22	−1.24	0.2285
Matrix \times size	−3.42	1.23	22	−2.78	0.0108

† Underlined variables are in the intercept.

‡ Values are on the logit scale.

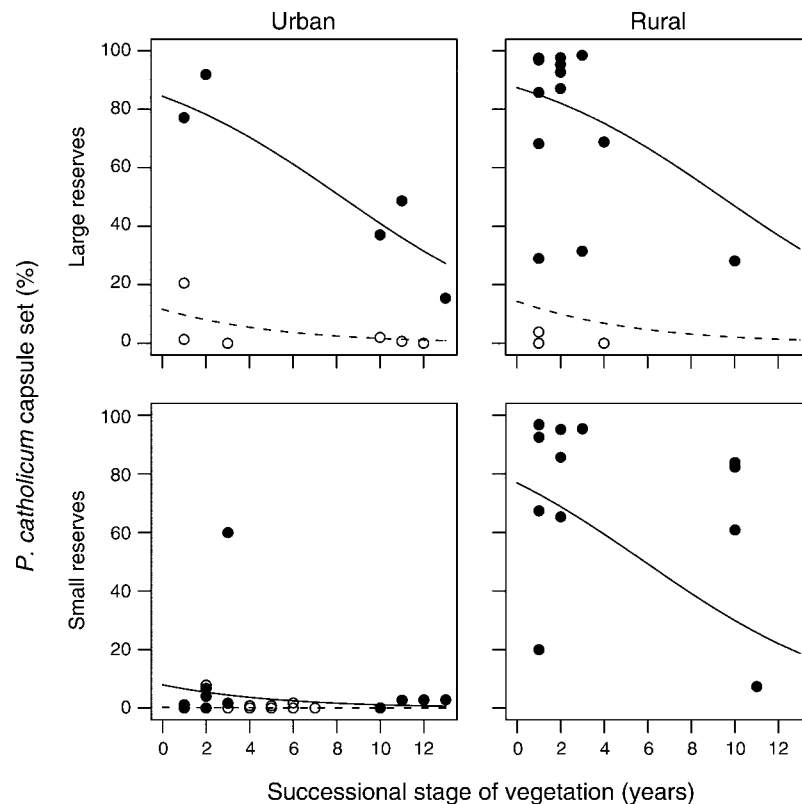


FIG. 4. Capsule set in *P. catholicum* in relation to the interaction between four explanatory variables. Open circles are sites located on sandy soils; solid circles are sites located on clay soils. Dashed lines (predictions for sandy sites) and solid lines (predictions for clay sites) are generated by a generalized linear mixed model (Table 1). Capsule set decreased with increasing age of the vegetation and was lower on sandy soils. Anthropogenic impacts can be detected against this background pattern of naturally occurring variability. Capsule set was lower in small nature reserves if these were located in an urban matrix.

specialist plant species that it pollinates (Figs. 4 and 5). This result is consistent with the idea of an unfolding pollinator crisis caused by the early loss of generalist pollinators followed by a cascade of linked declines (Gilbert 1978, Cox et al. 1991, Buchmann and Nabhan 1996, Kearns et al. 1998). The study demonstrates the utility of the pollination web approach in studies of anthropogenic impacts on pollination, and complements theoretical developments (Bascompte et al. 2003, 2006, Ashworth et al. 2004, Vazquez and Aizen 2004, Fortuna and Bascompte 2006), and an experimental study in which this approach has been used (Fontaine et al. 2006).

This study provides evidence for regional declines in pollination by wild pollinators, adding weight to recent reports of regional declines in flower-visiting insects (Biesmeijer et al. 2006). However, detecting these declines in pollination rate is complicated by substantial natural variability, which typically occurs at a regional scale. In this study, seed capsule set in the orchid *P. catholicum*, which is a good proxy for the pollination activity of *R. peringueyi* (see *Results* and Figs. 2 and 3), decreased significantly with increasing postburn age of the vegetation, and was very low, or zero, on sandy soils

under all circumstances (Table 1, Fig. 4). These natural patterns are interesting. Low pollination rates in late-successional vegetation demonstrate a benefit of fire-stimulated flowering, while low rates of pollination and seed set in sandy areas suggest a metapopulation dynamic between areas with clay and areas with sandy soil. From an evolutionary perspective it is significant that some pollinators are confined to particular soil types, because it suggests that plant populations that establish on novel soil types will experience new selective pressures on both vegetative and floral features simultaneously.

Recent anthropogenic impacts on pollination were detectable against this non-anthropogenic pattern of background variability in pollination. The size of the conservation area and use of the surrounding land interacted to produce a significant effect: capsule set was depressed in small conservation areas in an urban matrix (Table 1, Fig. 4). This result raises concern because it suggests that many proclaimed conservation areas are not large enough to protect biotic interaction. Signal Hill, an isolated 385-ha portion of the Table Mountain National Park (Pauw and Johnson 1999), was the largest conservation area where the failure of the *R. peringueyi*

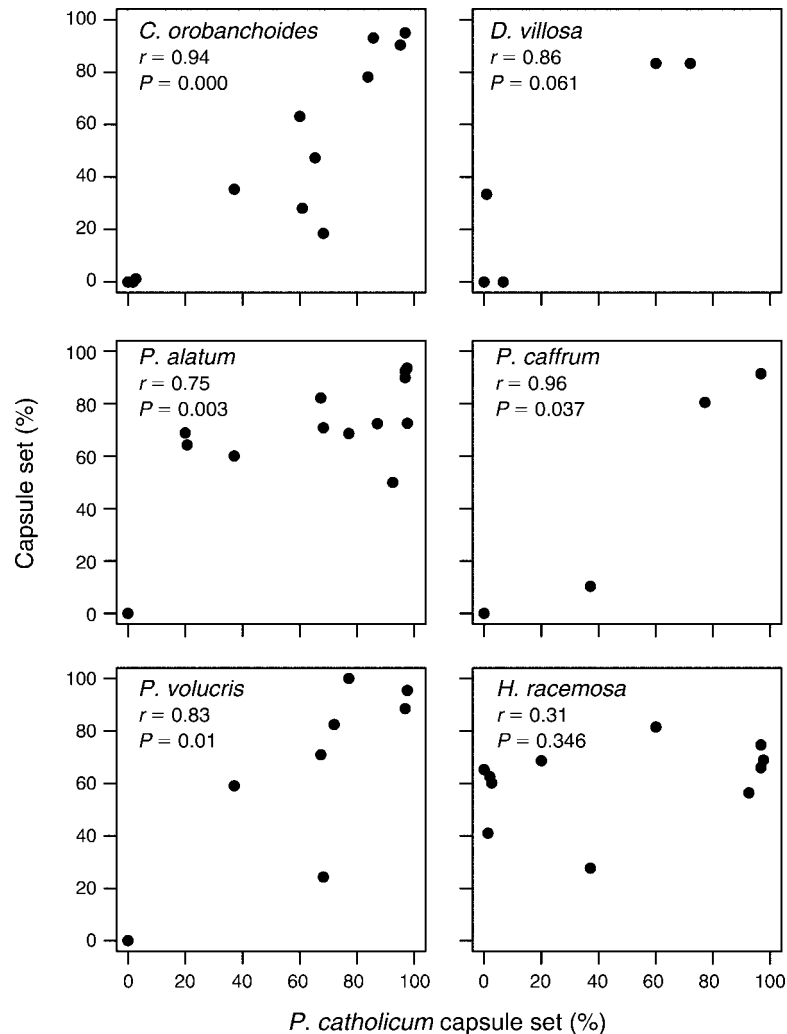


FIG. 5. Correlated reproductive success across sites indicates a cascade of linked declines among the members of the *R. peringueyi* pollination community following pollinator loss. *P. catholicum* and the first five species have *R. peringueyi* as their sole pollinator, and the absence of this pollinator from some conservation areas results in unanimous reproductive failure. The sixth species, *H. racemosa* is pollinated by *R. peringueyi*, but also by several smaller *Rediviva* species, which are particularly important at sites where *R. peringueyi* is absent.

pollination system could be attributed to habitat fragmentation by urbanization, rather than to natural causes.

In contrast, small conservation areas in a rural matrix did not suffer anthropogenic pollinator loss (Fig. 4). A rural matrix (which in this study included biodiverse pastures and fallow fields) may still allow pollinator movement between conservation areas (Murren 2002, Tonhasca et al. 2003). The implication is that fragments of natural vegetation in a biodiverse agricultural matrix are not islands from the perspective of *R. peringueyi* (Jules and Shahani 2003). Increasing agricultural use in the matrix may, however, soon lead to the insulation of these reserves and the concomitant collapse of the *R. peringueyi* pollination web.

Consistent with the idea of cascades of linked declines (Gilbert 1978, Cox et al. 1991), the loss of a generalist pollinator, *R. peringueyi*, from conservation areas precipitated a decline in seed set among several linked specialists for which data were analyzed (Fig. 5). Additional observations of species not included in this study suggest that this result is probably more general. For example, reproduction was monitored in one population of the endangered, oil-secreting orchid *Pterygodium cruciferum*, a species probably pollinated by *R. peringueyi* (Pauw 2006). Capsule set was zero in three successive years (323, 141, and 142 flowers; Site 12), and was matched by reproductive failure in *C. orobanchoides* and *P. catholicum*, which co-occurred at the site. While data on rare species might be difficult to obtain, correlated patterns of capsule set indicate that

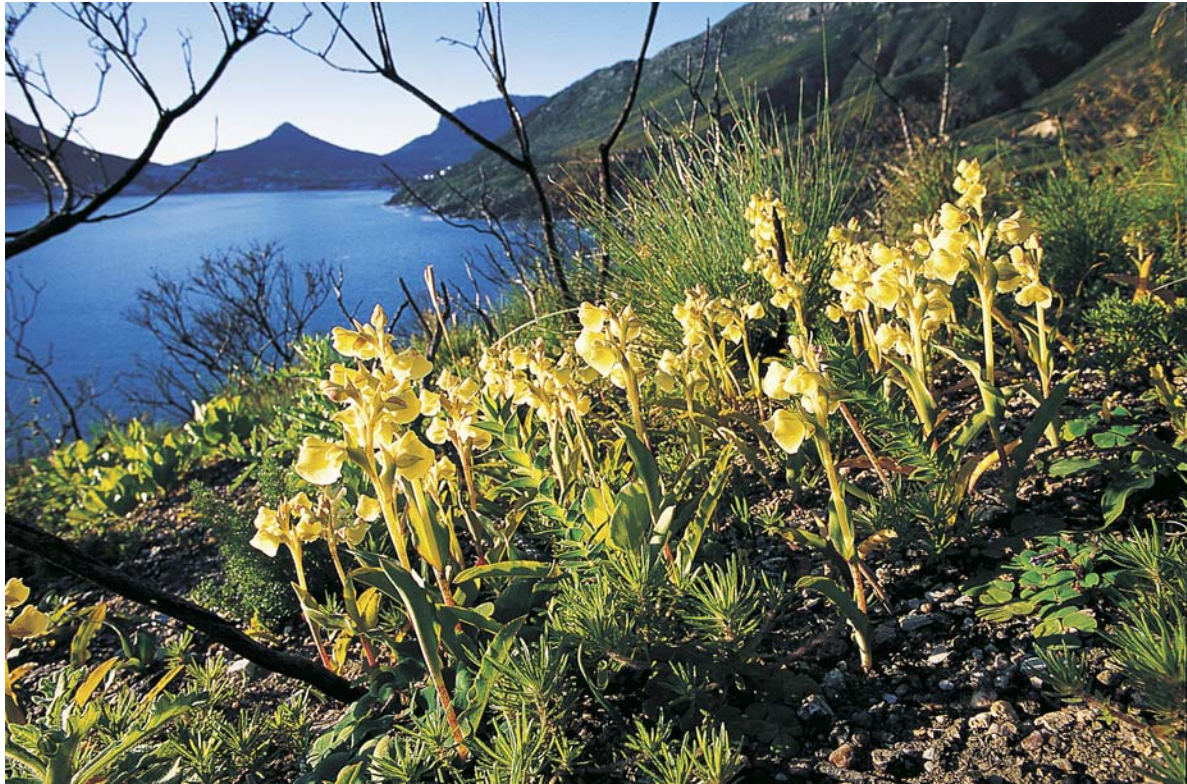


PLATE 1. Oil-secreting orchids (*Pterygodium catholicum*) flowering in the first spring after a fire on the slopes of Chapman's Peak, Cape Peninsula, South Africa. Photo credit: A. Pauw.

pollination webs are in some instances so tightly integrated that seed set in one common plant species might be monitored as an indicator of community-wide pollination rates.

The pollination generalist *H. racemosa* (Scrophulariaceae) was the exception to this pattern of correlated declines in seed set (Fig. 5). As predicted, generalization buffers this species against the effects of pollinator loss (Bond 1994). In conservation areas where *R. peringueyi* was absent, other *Rediviva* species were observed to act as effective pollinators and seed set remained high. However, at some sites not included in this study, all *Rediviva* are absent and seed set in *H. racemosa* does decline (Pauw 2005).

It would be interesting to investigate further the mechanisms by which the predictor variables included in this study act on pollination rate. Density of flowers is an important determinant of pollination rate (e.g., Wagenius 2006). In this study system, the density of oil-secreting flowers declined sharply as succession proceeded and the shrub canopy closed over, so it seems likely that successional stage acts on pollination rate via its effect on the density of oil resources. Since small conservation areas will often contain only late-successional vegetation, it is important to determine whether *R. peringueyi* individuals move on, or remain in diapause during the interfire period (e.g., Danforth 1999).

The density of oil-secreting flowers seems less likely to determine the differences in pollination rate observed between sandy and clay soils. At least at the intermediate scale (9×9 m plots), the density of *P. catholicum* is consistently high in areas with sandy and clay soil (Appendix B). Instead, unconsolidated, sandy soils may be unsuitable for nest construction by *R. peringueyi*, and thus soil type may act directly to determine the abundance of this ground-nesting bee (Gess and Gess 1993, Vinson et al. 1993, Westrich 1996, Cane et al. 2006).

Throughout this discussion I have focused on the availability of oil resources and the needs of female bees. It should, however, be borne in mind that habitat fragmentation, soil type, and the successional stage of the vegetation may affect *R. peringueyi* populations by initially affecting male bees or the shallow-flowered nectar plants that both male and female bees visit (Whitehead and Steiner 2001, Pauw 2006).

The consequence of the collapse of the pollination web for plant population persistence is the topic of future work. However, for the sake of the argument presented here, it is necessary to say that the densities of the two most abundant oil-secreting species, *P. catholicum* and *H. racemosa*, are unlikely to have declined in the period following pollinator loss, since neither species has a high level of dependence on *R. peringueyi* for

population persistence. *P. catholicum* forms long-lived, clonal colonies through extensive vegetative reproduction (Pauw 2004), while *H. racemosa* is partly autogamous and has a relatively generalized pollination system (Pauw 2005).

In conclusion, the loss of a generalist pollinator has been shown to trigger a cascade of linked declines in seed set among the community of linked specialists. The pollination web considered here is simple, but has many significant features, such as asymmetrical specialization and pollinator-dependent seed set, in common with larger and more complex pollination webs (Bascompte et al. 2003, Ashman et al. 2004, Vazquez and Aizen 2004, Knight et al. 2005). While anthropogenic impacts on more complex systems might be more difficult to detect, it seems premature to dismiss the possibility that pollinators are important and fragile nodes in the web of life.

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APPENDIX A

A table presenting capsule set data for *Pterygodium catholicum* collected over four years in 27 conservation areas that varied in size, the matrix in which they were located, soil type, and the postfire successional stage of the vegetation (*Ecological Archives* E088-104-A1).

APPENDIX B

A table listing the density of *P. catholicum* ramets observed across a range of sites (*Ecological Archives* E088-104-A2).