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Conservation issues from research on pollination ecology - a West Mediterranean view

Abstract

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The assessment of endangered plant species is commonly performed by evaluating, among other things, the decrease in the quality and quantity of pollination services under global change parameters. This allows inferences to be made about declining pollination success, reduced genetic diversity and the low recruitment performances of descendants. Although most case studies on the pollination ecology of threatened Mediterranean species show no clear evidence of pollinator decline, negative consequences are commonly expected. In this article we review data from our own research and the literature in order to survey experimental approaches to assessing the true threat posed by pollination deficit. We report on documented cases of endangered plants – mainly from the W. Mediterranean - with limited pollination. Current conservation efforts are also outlined and further lines of research proposed.

Introduction

The conservation issues related to pollination ecology comprise a complex web of interacting factors in global change, beginning with the general context of climatic change. The trends projected by the United Nations, which have recently been endorsed by the European Environment Agency, are towards increasing average temperatures, changes in the distribution of precipitation and associated alterations (UNEP 2003; EEA 2004) (Tab. 1). These documents include projected impacts on biodiversity: mutualisms, including pollination, are under severe threat, both through risk of extinction of keystone species, and through a projected disruption of plant-animal interactions caused by differential responses to climatic changes (EEA 2004) (Tab. 2). Summaries of species and their interactions have been published by Kremen & Ricketts (2000), Thomas & al. (2004), Pounds & Puschendorf (2004), and some case studies on specific areas indicate that these changes have already begun in many parts of the world (Primack & al. 2004), including the Mediterranean area (Gavilán 2001; Peñuelas & al. 2002). Thus, the expected consequences of climatic changes on mutualistic assemblages, such as pollination, are predictable, though not yet fully confirmed.

Table 1. The summary of projected changes in Global and European climate (Sources: United Nations Environmental Program 2003: 41-42; European Environmental Agency 2004: 1-8).

PARAMETER	PROJECTION
CO_2 concentration	540-970 ppm (2100) [280 in the pre-industrial era; 368 in 2000]
Sulfate aerosol concentrations	Fall below present level by 2100
Average temperature	Globally: projected increase of 1.4-5.8ºC (1990-2100) Europe: projected increase of 2.0-6.3ºC (1990-2100) Changes in variability (daily, seasonal, inter annual, and decadal)
Average annual precipitation	Globally: projected increase. Regionally: ± 5-20% N. Europe: 10-40% wetter S. Europe: 20% drier
Glaciers and ice caps	Continued widespread retreat during the 21st century By 2050 c. 75% of Swiss Alps glaciers are likely to disappear
Global sea level	Rise by 0.09 to 0.88 mm/year (1990-2100) Around Europe by 0.8-3.0 mm/year x 2.2-4.4 (21st century)

However, in some regions, the relative impact of climatic change is likely to be lower than that of other factors. Pollination systems are under increasing threat from more direct anthropogenic sources, including habitat fragmentation, changes in land use, modern agricultural practices, use of chemicals (such as pesticides or herbicides), and invasions of non-native plants and animals, independently of (or in addition to) climatic considerations. The effects of human activities on pollination systems have lead to the so-called "pollination crisis" (Buchmann & Nabhan 1996; Kearns & al. 1998). One of the major factors in this crisis is the decline in pollinators (see Goulson & al. 2005), which some authors consider as environmental bioindicators (Kevan 1999).

Table 2. The summary of projected impact on individuals, populations, species, and ecosystems (Source: United Nations Environmental Program 2003: 45).

PARAMETER	PROJECTION
Species losses	Increase
Extinction of wildlife populations	Increase (particularly pronounced when a population is isolated by habitat loss)
Changes in phenology	Expected to continue
Habitat displacement	Move upward / poleward from current locations (accelerated by anthropogenic disturbances) *2100: 200-1200 km northward for temperate and boreal plant species. New species assemblages?
Ecosystem interactions	Disruption, species unlike to shift together
Critical / vulnerable life stages	Expected to continue to affect
Populations, species and ecosystems vulnerable to climate change 1. Species/ecosystems with limited climatic ranges and/or restricted habitat requirements 2. Species already in risk of extinction	

The loss of pollination services, besides affecting their contribution to reproduction and the maintenance of evolutionary processes of plant biodiversity, can also be evaluated in economic terms. In fact, the pollination of flowering plants by animals is a critical ecosystem service of great value to humanity (Kearns & al. 1998). World pollination services in wild ecosystems have been estimated to have a mean value per annum of 112$ billion (Costanza & al. 1997) and 200$ billion in global agriculture (Richards 1993). Marco & Monteiro (2004) demonstrated the positive effects of forest conservation to preserve native pollinators, which are increasing coffee production in Brazil. The United Nations FAO programmes also confirm the essential services provided by pollination (http://fao.org.biodiversity/pollinat_en.asp).

Claims of widespread decrease in animal pollinators and pollination decline have captured public and scientific attention in the last decade (Thomson 2001). The economic importance of pollination and its biological value makes the conservation of pollination systems a high priority.

Summary of threats to pollination systems

In our research on pollination ecology in W. Mediterranean systems, we have detected several types of endangered mutualisms or pollination disturbances that correspond to the main classes of threat to the pollination systems previously summarized by other authors (similar data are available from the E. Mediterranean region, see Petanidou & Ellis 1996; Petanidou 2004, 2005; Potts & al. 2002, among others).

Effects of agricultural practices

Several features of modern agriculture provide poor habitats for wild pollinators. Crop monocultures decrease floral diversity and the heterogeneity of pollinating agents (Pywell & al. 2005). A decrease in marginal areas (due to cultivation or transformation) results in a loss of wild vegetation to support pollinators (González 2004): fewer nesting areas for bees; fewer larval host plants for butterflies and less-varied habitats for egg laying and larval development have been the most cited effects (Kearns & al. 1998; Carvell & al. 2001; Pywell & al. 2005; Goulson & al. 2005). In some Mediterranean countries, this situation has begun to reverse, through the abandonment of agricultural fields and subsequent ecological changes, producing new successional phases leading to shrub and forest recovery (Petanidou 2004).

Delphinium bolosii, an endangered species endemic to Catalonia (Bosch & al. 1998), provides evidence of the indirect effects of shrub recovery. In the smaller of the only two existing populations, cultivation of the hazelnut tree, *Corylus avellana*, was abandoned some years ago. This could be considered as an opportunity for the recovery of the endangered population that survives in a small ravine previously surrounded by agricultural fields. However, once cultivation ceased, progressively increasing densities of the shrub *Rubus ulmifolius* began to invade the refuge of the endemic larkspur. As a result, in addition to long-term competition for habitat resources, competition in attracting pollinators was observed between *D. bolosii* and *R. ulmifolius* (Orellana & al. 2004). The study of stigmatic pollen loads showed a total heterospecific load of 8 %, a high proportion of which was from *R. ulmifolius*. The effects of purity in relation to neighboring species were assessed by comparing pure and mixed plots. Slight negative effects on reproductive traits (such as higher rates of seed abortion (50%) and declining viable seed/ovules index) were detected as a result of interspecific competition for pollinators. In short, a disturbance effect was detected and thus conservation efforts were oriented towards the removal or control of *Rubus* in this population. Similar conclusions relating to grassland management in order to prevent shrub expansion are widely reported, and in some cases the benefits for plant-animal interactions are clear (Krauss & al. 2004).

Finally, pollinator loss could affect agricultural systems. According to Matheson & al. (1996), 84 % of crop species grown in the European Union are dependent on insect pollination, and declines in bee populations are widely reported in Europe (Kearns & al. 1998; Goulson & al. 2005, and references therein), as well as in America (Kevan 1974; 1995; 1998; 2001).

Grazing

Intensive grazing threatens pollinators through the removal of food resources, the destruction of underground nests and potential nest sites, and other subtle mechanisms (Kearns & al. 1998). Direct effects on the quality and quantity of pollen after loss of foliar surfaces caused by herbivory have also been reported (Aizen & Raffaele 1996). In recent years, grazing has directly damaged threatened plants in conservation programmes in the Mediterranean region. In most cases, this has occurred through the blocking of flower and pollen production, leading to a loss of plant sexual reproduction and subsequent seed set. However, grazing has also had indirect effects on pollinators by removing their food sources. In the recent Red Book of Spanish vascular plants, overgrazing was identified as the main source of threat for endangered plant species (c. 40 %, Bañares & al. 2003).

One of our findings on endangered species comes from the Pyrenean endemic larkspur *Delphinium montanum* (Simon & al. 2001). This subalpine larkspur presents the classical bee-syndrome of a specialized spur flower. In 1994, the flowers and stems of some populations in the Cadí Natural Park (Catalonia) were extensively grazed by chamois (*Rupicapra pyrenaica*). This predation of floral stems continued for 10 years with annual losses of 92-98 % of flowers. Similar findings were reported in the reserve of Noedes and Cambredase (French Catalonia) in summer 2004 (Simon pers. observ.). The long-term effects of this predation are unknown at present and pollination limitation (>90% decline) seems buffered by demographic characteristics, such as adult longevity or seedling recruitment (Aymerich 2003).

Additional reports from Spain confirm the increasing trend in floral predation by grazing, which is particularly significant in threatened species and within protected areas (Tab. 3).

Chemicals

Pesticides pose a major threat to pollinators, not only when applied to agricultural crops, but also in grasslands, forests, urban areas and tourist resorts (Kearns & al. 1998; Carvell & al. 2001). Although environmental regulations in industrialized countries have reduced pollinator poisoning, problems are still being reported in developing countries. Pesticides, directly applied or after pollinator foraging, can also affect honey and pollen, and several

Table 3. The effect of grazing by herbivores on flowering phases of some threatened species in Spain from recent literature: CAN - Canary Islands, ARA - Aragon, C-LM - Castilla-La Mancha, MUR - Murcia, BAL - Balearic Islands, CAT - Catalonia.

Taxon	Region	Predator	Affectation	Measures	Reference
Helianthemum juliae	CAN	Rabbits	Seedlings predation	Monitoring plan	Bañares & al. (1993)
Cistus osbaeckiaefolius	CAN	Rabbits and mouflons	Fruit predation	Monitoring plan	Bañares & al. (1993)
Echium acanthocarpum	CAN	Introduced animals (rabbits, mousses, goats)	New seedlings establishment	Fencing Recovery plan	Marrero & al. (2000)
Krascheninnikovia ceratoides	ARA	Sheep	Cycle interruption and consumption of juveniles	Prohibition of grazing in a population	Domínguez & al. (2001)
Stemmantha cynaroides	CAN	Introduced rabbits and mouflons	Flowers consumption	?	Fernández & Marrero (2000)
Erodium paularense	C-LM	Livestock	Flowers and fruits	Monitoring plan	Iriondo & al. (2001)
Anthirrhinum subbeticum	MUR	Grazing (non specified)	Flowers	Monitoring plan	Sánchez & al. (2002)
Narcissus nevadensis subsp. *enemeritoi*	MUR	?	Flowers and fruits predation	Monitoring plan	Sánchez & al. (2002)
Ligusticum huteri	BAL	Goats and sheeps	Flowers / Aging of populations	Fencing Monitoring plan	Vicens (2002)
Delphinium montanum	CAT	Chamois and moles	Flowers and stems (up to 95-100%). Short-time compensation by seed bank	Fencing Monitoring plan	Simon & al. (2001) Aymerich (2003)
Peucedanum schottii	CAT	Goats and sheeps	Flowers and fruits	Any	Molero & Rovira (ined.)
Salix tarraconensis	CAT	Hispanic goats	Branches, stems and flowers	Any	Baiges & Blanché (ined.)

chemicals (organic, heavy metals and radionucleotides) have been detected in these products. Herbicides also affect pollinators by reducing the availability of nectar plants and may have greater effects than pesticides. One example leading to massive pollinator decline is herbicide spraying in alfalfa crops (Kearns & al. 1998).

Biological agents

General declines in honeybee populations have been reported in several parts of the world, including the European Union. Infection by parasitic mites, introduction of non-native pollinators and competition with other native pollinators are among the causes cited (Kearns & al. 1998; Goulson & al. 2005, and references therein).

Regarding plants, pollination disturbances caused by the introduction of invasive species have also been reported (Morales & Aizen 2002). In the Mediterranean area, the Balearics (Spain) and Hyères Islands (France), the flowers of the introduced *Carpobrotus* *edulis* compete with those of native species such as *Lotus cytisoides*, *Anthyllis cytisoides* and *Cistus monspeliensis* for pollinator services (Travesset 2004). Pollinators may also act as vectors for carrying foreign pollen of related species, and are thus possible agents of extinction through hybridization / introgression caused by genome pollution of small populations.

Fragmentation

Finally, habitat fragmentation is a major threat to pollination systems: it is one of the main topics addressed in conservation biology today, both for species and species assemblages. Studies over the last decade have produced an increasingly complex model of the impact of fragmentation on plant populations.

Hobbs & Yates (2003) note that the direct effects of fragmentation, which are generally an inevitable consequence of habitat destruction, include: the creation of small patches, the alteration of landscape processes, the isolation of patches in an altered matrix, and the reduction of population sizes. These changes produce follow–on consequences for ecosystems and species, and these in turn can have a subsequent impact on plant populations, leading to decreased abundance and risk of extinction (at least locally) for particular species. Pollination takes place at the central and most vulnerable node of a complex network of biotic interactions. The controversial discussion on the causes of bumblebee declines by Goulson & al. (2005) and Williams (2005) highlights the difficulty in tracing habitat and pollinator interactions under the pressure of global change.

If, following fragmentation, the local pollinator declines within a fragment, the location of the fragment is outside the foraging range of pollinators, or wide-ranging pollinators avoid small plant populations or isolated fragments, then pollination services and reproductive potential can be expected to decrease. This may result in plant species decline (Kearns & al. 1998; Hobbs & Yates 2003).

Results from a survey on the endangered *Seseli farrenyi* (Apiaceae) (Rovira & al. 2004) show how some of the expected effects of fragmentation can be detected. *S. farrenyi* is a species endemic to a very narrow coastal strip of Cape Creus, in Catalonia. It is a good example of the effects of fragmentation on small populations because of its limited distribution and low number of individuals, and its progressive decline due to fragmentation. It is a highly unspecific entomophilous plant, visited by at least 28 insect species. In the smallest and most fragmented population, the stigmatic pollen loads of conspecific pollen and seed set are decreasing because of a rise in the percentage of visits by ants and coleopterans (which carry less pollen shorter distances). This failure to recruit adequate pollinator services as a result of habitat fragmentation has already been reported (Aizen & Feisinger 1994; Weller 1994). The resulting pollination disruptions in the small fragment lead to an increased risk of extinction through a complementary loss of genetic diversity of 18.7%, estimated by allozyme polymorphism (López-Pujol & al. 2002). This example of how pollination is involved in the web of disturbed interactions caused by habitat fragmentation is only one among the increasing number of cases reported by the literature during the last decade.

Pollination decline and plant species conservation: controversies

However, the concept of a “pollination crisis” and its consequences for plant species conservation is far more complex than one might initially assume. Although a number of studies report partial evidence of either absolute loss of pollinators or loss of quality or quantity of pollinator services, in both widespread and endemic or endangered plant species, some controversial studies have put forward new paradigms. These address compensating strategies for pollination loss, as well as other issues.

Linked extinction of plant and animal species

Firstly, relatively few plant-pollinator interactions are absolutely obligate if the complex web of possible interactions between plant species and flower-visiting animals worldwide is considered (Kearns & al. 1998; Kawakita & Kato 2004). Most are more generalized on the part of plants and animals, and they also vary through time and space, although this generalization shows some geographic patterns (Olesen & Jordano 2002). A Mediterranean example of temporal variation is *Seseli farrenyi* (Rovira & al. 2004), whose pollen deposition varies in the course of the flowering season (Fig. 1), while an example of spatial variation can be found in the specialized flowers of larkspurs (Bosch 1999), whose flowers are similar from southern France to northern Morocco, yet receive a great variety of pollinators depending on habitat (altitude, latitude) and the available fauna of pollinators (Tab. 4).

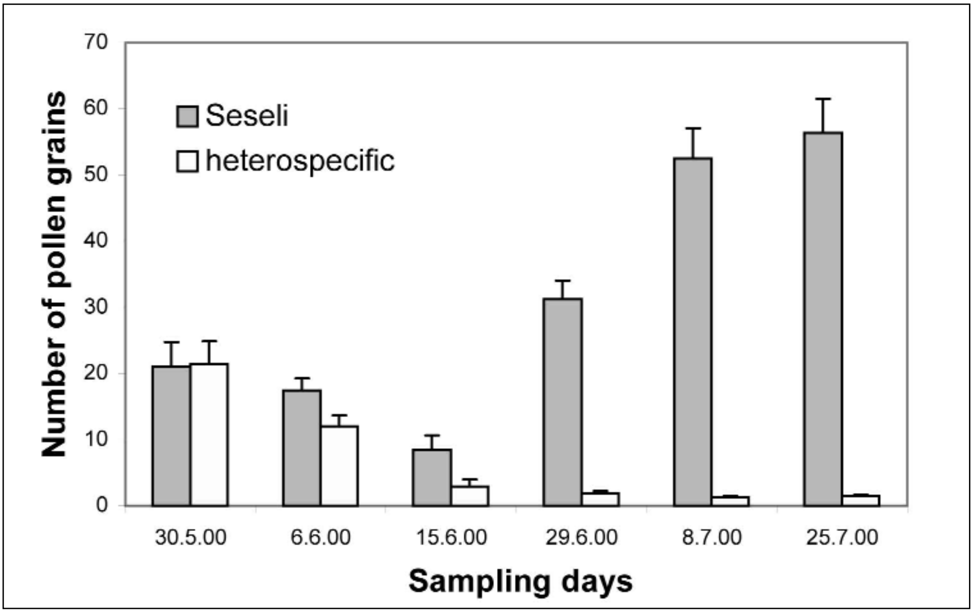

Fig. 1. Variation in pollinator activity across time in Mediterranean plants. Stigmatic pollen deposition during flowering period in *Seseli farrenyii* (from Rovira & al. 2004).

Table 4. The pollinator variation of larkspurs (*Delphinium* spp.) in the Western Mediterranean area across space from North to South (from Bosch 1999): R - robbers (<10% of visits), RR - robbers (>10% of visits); + - pollinators (<10% of visits), ++ - pollinators (>10% of visits); MON - *D. montanum* (1: Ga: W. Pyrenees; 2: Hs: Cadí range), BOL - *D. bolosii* (1: Hs: Lleida; 2: Hs: Tarragona), STA - *D. staphisagria* (1: Hs: Alacant; 3: Bl: Eivissa), PIC - *D. pictum* (2: Bl: Mallorca), VER - *D. verdunense* (1: Hs: Barcelona; 2: Hs: Girona), GRA - *D. gracile* (1: Hs: Osca), BAL - *D. balansae* (Ma: Meknès), OBC - *D. obcordatum* (1: Ma: Tétouan), FAV - *D. favargeri* (Ma: Marrakech).

Pollinators	*Delphinium*												
	MON1	MON2	BOL1	BOL2	STA1	STA3	PIC2	VER1	VER2	GRA1	BAL1	OBC1	FAV1
HYMENOPTERA													
Apidae													
Bombus hortorum	++	++											
Bombus wurfleini	RR												
Bombus terrestris			RR	R			++		++			++	
Bombus pasquorum			+	+			+	+	+				
Anthophoridae													
Amegilla sp.						++		++	+		++	++	++
Anthophora dispar			+										
Xylocopa violacea			++				+			R			
Megachilidae													
Oplitis sp.						++							
Megachile rotunda						++							
Halictidae													
Lassioglossum sp.			+	++	++			++	+	++	++		
Halictus sp.				+				+	++				
Eumenidae													
Alastor atropos			R	RR				+		RR			
LEPIDOPTERA													
Macroglossum stellatarum	+		++	+	++	++	++	+	+		+	++	
Others	+		++	++				++	++	+		+	+
DIPTERA													
Bombylius sp.			+	+					+	+		+	
Syrphidae	++	++	+	+	++	+	++	+	+				++

Altitude (in m)	1980	2350	290	600	150	160	100	196	50	300	1930	5	1300
Flowering (months)	Jl-A	Jl-A	J	J	My-J	My-J	J	Jl-A	Jl-A	Jl-A	J-Jl	J-Jl	J-Jl

Thus, the recognition that most pollination interactions are not obligate necessarily changes our approach to their conservation. We should abandon the notion that losing one plant species implies the loss of one or more animal species via linked extinction and vice versa (except for few relevant but scarce examples and bearing in mind the recent view of possible asymmetric specialization of plant-pollinator interactions by Vázquez & Aizen 2004). If pollination "interaction webs" are relatively richly connected and shift in time and space, depending in part on the landscape context, then the work of conservation biologists is made still more complex.

Plant species extinction caused by loss of pollination

Surprisingly, for a substantial proportion of the most endangered species, significant pollination losses are not reported as the basis of the threats to their survival. Evidence of this comes, for instance, from the data given by the Red Lists from the western Mediterranean, where the nature of these threats is detailed.

Of the species listed as extinct in France (Olivier & al. 1995), Catalonia (Sáez & al. 1998; Sáez & Soriano 2000), the Balearic Islands (Sáez & Rosselló 2001) or Spain (Bañares & al. 2003), habitat degradation/destruction is responsible for most cases, followed by changes in land use and unknown causes. However, pollination or reproductive failure is not mentioned. More interestingly, the review of threats affecting the more than 2,223 populations surveyed, which belong to the 478 most endangered species in Spain (Bañares & al. 2003), reveals that the main cause of threat is overgrazing (c. 40%). Reproductive strategies are responsible for less than 10% of documented threats to endangered populations.

There is little literature on plant species that have become extinct through reproductive limitations, and specifically pollination limitation, although some cases have been described involving the absolute loss of pollinators. These include *Ixianthes*, a South African shrub belonging to Scrophulariaceae (Steiner 1993) or *Freycinetia baueriana*, a liana from New Zealand which lost its bat pollinator (Lord 1991).

The scarcity of documented extinctions through pollinator losses can be put down to a) a need for more extensive research on plant-pollinator interactions or, b) the recognition that there are no direct and immediate effects on plant reproduction, but that more subtle and slow-paced processes are taking place, whose long-term effects may be more serious than expected.

Fragmentation research does not allow generalization

Some authors (Cane 2001; Hobbs & Yates 2003) have recently questioned the view that habitat fragmentation necessarily results in a widespread collapse of plant-pollinator interactions, except in the most extreme cases. Pollinating insects may show differing responses to the same fragmentation/disturbance regime (Williams 2005).

Cane (2001), for example, proposes that the effect of habitat fragmentation on honeybees depends on the spatial distribution of resources in the new landscape and the decline of the permeability of the matrix (Fig. 2). In the first scenario (Fig. 2A), following fragmentation, the distribution of resources and nest sites forms a disrupted web broken by disturbances or discontinuities, and only a few populations are pollinated (a single population in the example). However, if the patchiness of the resources in the new landscape is within the foraging range of the bee and the matrix is permeable, fragmentation may have little impact on the pollinator (Fig. 2B). A good example can be found in the Panama Canal, where plant species import pollinators from outside each fragment (island pollinator nesting sites are disappearing but pollinators from mainland forest continue to pollinate effectively) (Murren 2002).

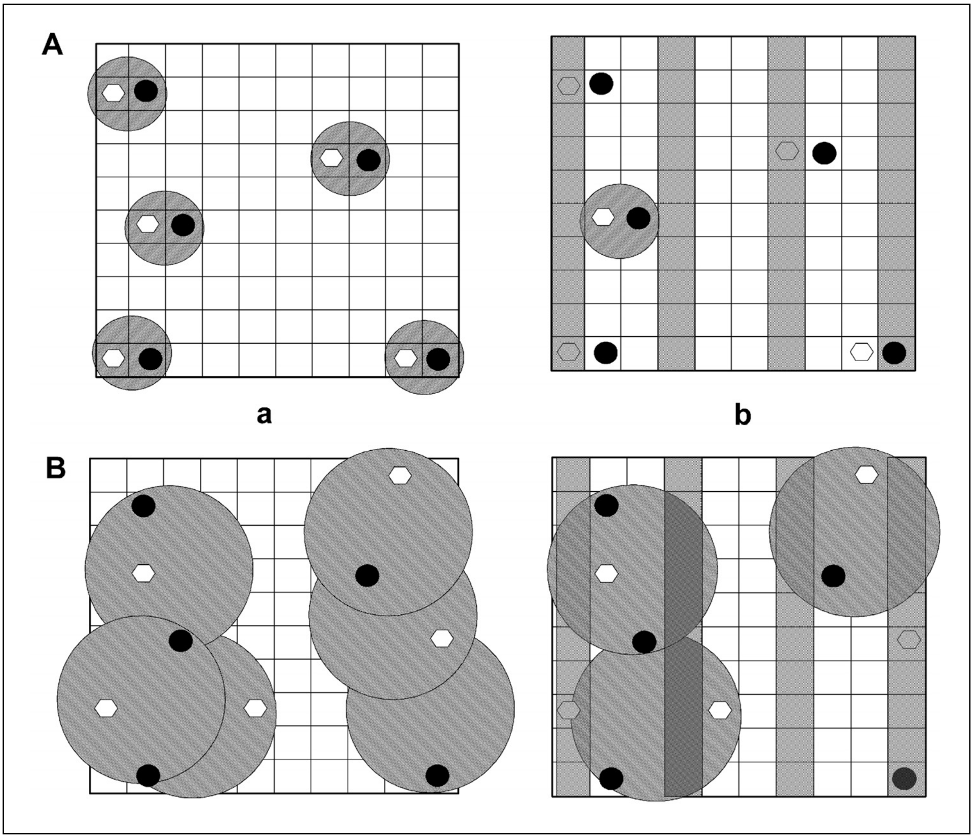

Fig. 2. Will habitat fragmentation result in a widespread collapse of plant-pollinator interactions? In a permeable matrix, the same fragmentation pattern (grey bars) produces distinct effects on 5 plant populations (black dots), depending on an interacting set of attributes (time and space distribution of resources on the fragments, pollinator search behaviour and diet breadth). Hexagons represent nesting sites and circles foraging range of pollinators. (a, before fragmentation; b, after fragmentation). A) Narrow foraging range (1 single population remain served). B) Wide foraging range (4 populations remain served).

Moreover, depending on the life history of pollinating insects, their responses to similar fragmentation patterns may also differ, with some species declining and others increasing in abundance (Davies & al. 2000; Donaldson & al. 2002) according to an interacting set of attributes. Of special interest in the Mediterranean is the effect of fire on pollination systems, recently reported by Ne'eman & al. (2000) and Potts & al. (2003) but with particular adaptive features in fire-dependent ecosystems (Hiers & al. 2000).

Empirical studies on the impact of fragmentation on insect pollinator communities have reported a wide range of results, from extremely sensitive to highly resistant / resilient responses. All these studies show that it is difficult to generalize about the effects of fragmentation on pollinator abundance.

Research on pollination and seed set declines

When no clear evidence of a direct relationship between pollination failure and plant losses is obtained from the above conservation sources, then the underlying processes of pollination disruptions may not be detected by the extensive (but not always in-depth) Red List surveys. The general hypothesis, taken from Aizen & Feisinger (1994), indicates that “As fragments and populations become smaller and more isolated, rates of visitation by pollinators and plant fecundity will decline”. Several mechanisms have been postulated to explain this hypothesis, such as:

Pollinator diversity and abundance decline within fragments as they become smaller and more isolated, which results in fewer visits and lower seed set (Bosch & al. 2003).

Because pollination is a density-dependent process (Kunin 1997), small populations created by fragmentation may be less attractive and receive fewer visits, which results in a smaller seed set (Jennersten 1988).

As populations become smaller so too do genetic neighborhoods, which results in fewer mates for self-incompatible plants and increased inbreeding, both leading to a reduced seed set (Young & al. 2000).

The above hypotheses have been tested in several ways: a) by measuring the number of insect-flower visits and fecundity across fragments; b) by measuring pollen loads on stigmas, pollen tube abundance in flower styles and fecundity across fragments, and c) by comparing fruit or seed set in hand-pollinated and open-pollinated plants across fragments.

In some cases of fragmented populations of endemic species in the W. Mediterranean, our results show that all three methods are applicable and, to some degree, conclusive that a loss of pollination quality or quantity occurs, thereby decreasing genetic diversity in small fragments (Bosch & al. 2003). In a wider context, however, it is interesting to point out that from the results of all three approaches, the literature (reviewed by Hobbs & Yates 2003) reports mixed results: true and significant decline, balanced or non-significant results, and even an increase in the resulting fecundity.

Finally, some apparently contradictory results are open to discussion from the methodological point of view of the assessment of pollination declines.

How to fully document pollination declines

Some authors who examine pollinator declines (Thompson 2001, Wilcock & Neiland 2002, and the current authors), frequently discuss pollination deficits either as evidence that a decrease has occurred or as a possible negative consequence of future reductions. Because these deficits can be measured in short-term studies, these studies would be a better alternative to the documentation of insect population trends. In fact, shortages of pollinators and shortfalls of seed or fruit production are two aspects of the same problem, but for botanists, the plant perspective is to be preferred. Pollination deficits are detected mainly through pollen supplementation experiments, although pollinator supplementation can be preferable in the case of some crop plants.

Some reviews of hand-pollination experiments are available. In 62% of the natural populations studied, fruit or seed sets are limited by insufficient pollen at some times (Burd 1994). Similar percentages (59%) have also been found in crop plants (Mayfield 1998).

However, other research on threatened plants (Tepedino & al. 1999) shows much lower rates of pollination deficits (10-15%), which indicates that intact natural systems reach an evolutionary equilibrium in which reproduction is limited equally by pollination and by maternal resources. In other cases, apparent pollination limitation (only 5-10 % of fruit set) is not recovered after hand-pollination because of genetic loads or other primary causes. Furthermore, the dramatically lowered (1,000 fold) seed set after pollen supplementation in the rare *Oxyanthus pyriformis* in South Africa is directly related to the loss of the pollination services provided by the hawkmoth (Johnson & al. 2004). Indirect approaches using other evidence, such as the availability of nectar rewards (Jacquemyn & al. 2005), are also non-conclusive. Consequently, the contribution of pollination in determining plant population viability remains to be elucidated.

From our experience and from the cited reviews, several questions regarding the assessment of pollination deficits are still open to further research:

a) What is the optimum level of "natural" pollination? (other than hand-pollination. To fully demonstrate a decline we must first define the "standard" pollination level).

b) Are the populations selected for the study the most suitable? (in practice, we usually look for easily accessible and rewarding populations: results of very low visitation rates are frustrating to some extent and sometimes difficult to publish).

c) What is the smallest pollination deficit that can be detected with a given experimental design?

d) Is more pollen always better? (certain reported deficits could be reinterpreted as simply maintaining an equilibrium between a theoretical maximum of seed set and the available resources).

e) In the pollinator supplementation experimental approach, some methodological considerations - such as the non-linear effects of pollinator visitation rates – should be taken into account.

f) Pollination deficits should be placed in the context of plant life histories, so as to recognize that pollination failure can be buffered by alternative processes such as autogamy, agamospermy, wind pollination and vegetative propagation. This buffer effect is accepted in the case of long-lived perennials (Silvertown & al. 1993, 1996; Bosch & al. 2002). But conversely, there is also evidence that in annual and short-lived perennials, a reduction in seed set caused by pollinator deficits may lead to decreased population size and increased probability of extinction (Groom 1998; Lennartsson 2002).

In short, although theory and a number of studies propose that pollination disturbances or failure lead to lower profiles of sexual reproductive success, several methodological and theoretical issues call for further research. The enormous diversity of plant-animal interactions in our changing world will not make this an easy task.

Pollination systems conservation

Efforts to restore pollination systems are still at a preliminary stage, at least in Mediterranean countries. However, an increasing number of organizations are beginning to promote additional research and practical pollination restoration.

But let us conclude with Kremen & Ricketts (2000) that "pollination systems may never be restored to pristine, pre-human states" because global change will continue to: a) increase the length of the growing season, b) increase the northward movement of plant species at different rates to their pollinator webs, c) decrease and fragment both plant and pollinator populations, and d) introduce invasive weeds, exotic pollinators and non-native crops into natural ecosystems.

As Roubik (2001) suggests, the key question is whether these new systems can absorb new species and novel interactions. The challenge for conservation biology (and pollination conservation) is to understand both native and disrupted pollination systems in order to manage for pollination function over dysfunction. While we attempt to change the key factors of global change (overpopulation, over-consumption, changes in land use, disturbance regimes, climate), measures should be taken to slow the deterioration in biodiversity (Ehrlich 2003). These include:

- Scientific contributions: providing scientific information for conservation purposes and developing areas for further research, such as: the ecology of animal pollinators other than commercially important insects; the links between pollination and plant population dynamics; or the link between pollination disruption mechanisms and pollination under disrupted pollination web systems, including compensation processes for pollination failure in order to design potential management solutions.

- Pragmatic contributions: capacity to act in priority and urgent cases of threat but also to promote applied research for conservation purposes. This implies that recovery plans should include associated research on the management of threatened species among their goals, in addition to the strict recovery of demographic standards (i.e. number of individuals). Even if the biological aspects of a recovery plan fail, it still gives us the opportunity to obtain relevant biological information on endangered species if it is appropriately designed as an experiment. Basic ecological research on plant-pollinator interactions can be applied successfully to landscape management practices (Potts & al. 2001).

Some conservation activities are fine scale, as befits the requirements of locally endangered species or populations, whereas others address large-scale problems concerning widespread habitats or entire regions.

Fine scale

Some examples are given below to show conservation efforts focused on pollination at fine scale (specific plant/pollinator systems, certain agrosystems, population- or locality levels), some of them belonging to extremely endangered mutualisms, where a particular species, group of populations or single population has almost lost the ability to pollinate.

Maintenance of populations and species under complete pollination failure

Absence of pollinators. There are few examples of absolute loss of pollinators. However, in this case, at least in the short term, hand-pollination of plants may prove fruitful for conservation and a number of recovery plans have employed artificial pollination. Alternatively, exotic pollinators can be introduced, although this practice implies certain risks. Some examples have been reported in New Zealand (introduction of bumblebees to pollinate red clover) and Malaysia (introduction of weevils to pollinate oil palms) (Kearns & al. 1998).

Pre-flowering disruption. This is an extreme situation in which pollination does not take place because there are no available flowers. Some conservation activities directly address vegetative propagation, although in some cases the assisted complete rebuilding of the biological cycle requires supplemented pollinations (Shiau & al. 2002). These interventions must be limited to extreme cases of economic or symbolic importance, mainly because of the limited resources available for conservation. However, there is intense debate on the ethics of hand-pollination, as can be followed in Internet forums on wild orchids, for example. Other examples of pre-flowering disruption causes of reproductive failure are the result of genetics or difficulties in gamete production not directly related to pollination (Wilcock & Neiland 2002).

Coupled management of plant habitats and pollinators

In recent years, conservation activities have been more focused on habitat, ecosystem and regional efforts than on single-species targets (although some caution is needed in the case of multispecific recovery plans, as recently suggested by the Society for Conservation Biology [Clark & Harvey 2002], since multipack plans often pay little attention to the conservation needs of individual species). Pollination should benefit from this change of perception, which considers endangered plant populations as part of a web of interactions.

From this point of view, a good alternative is to promote, at local level: a) the maintenance of pollinators, b) habitat management for appropriate nest sites for bumblebees and for floral diversity to provide nectar and pollen (other plant species supporting services to small populations) and c) the conservation of marginal areas (in many parts of the world this may imply conservation of man-made habitats – as in the Mediterranean –, some of which are good substitutes for threatened or destroyed natural habitats).

Reintroduction of plants and pollinators

A particular case of the integrated management of the habitat of endangered plant species is the coupled reintroduction of plants and pollinators. If reintroduction of endangered plants is still relatively uncommon, few plant reintroductions to date have been stimulated by the need to support pollinators (although existing pollinators may have benefited, Kearns & al. 1998). A case of an insect-oriented action plan can be found in the small Columbrets Islands (Valencia), where the few remaining *Chrithmum maritimum* patches - on the verge of extinction - were reinforced, as they constitute the basic habitat of the endemic and endangered coleopteran *Morbidistella columbretensis* (Laguna 1998).

In plant reintroduction, the absence of native pollinators may be a serious limitation, particularly when the plant has a single pollinator species (but this obligate mutualism is infrequent, see above).

Changing agricultural practices

Some changes in agricultural practices can address both local and widespread problems. These include (briefly): a) Restrictions on the use of pesticides, herbicides and fertilizers, (though this does not automatically lead to the recovery of pollinator abundance if preceded by years of intensive land management; Fussell & Corbet 1992); b) Removal of alien pollinators and c) Domestication of wild bees and other pollinators.

Pywell & al. (2005) conclude that the promotion of marginal areas to develop natural revegetation provides habitat and resources that allow the recovery of pollinator populations. The persistence of a reticulate corridor system (as opposed to extensive open fields) of hedgerows, ditches, green lanes or tracks in semi-natural or rural areas is directly correlated with higher diversity and density of butterflies and bees (Croxton & al. 2005).

Large scale

Below we summarize four ambitious programs, including scientific- and pragmatic-oriented projects that represent large-scale approaches to the problems related to Pollination Conservation. International concern about the conservation of pollinators and pollination systems was expressed at the Third Conference of the Parties (COP 3) of the Convention on Biological Diversity, held in 1996, and in the subsequent São Paulo Declaration on Pollinators (http://www.biodiv.org/agro/pdf/pollinator/Pollinator-Report.pdf).

Migratory Pollinators Project

This project, promoted by the Arizona-Sonora Desert Museum, focuses on 4 species of pollinators (bats, hummingbirds and butterflies) that follow annual "nectar corridors" between Mexico and the US. In the first phase, the aim is to identify a model for spatial and temporal patterns of flowering phenology and pollinator migrations. Gaps in these corridors will indicate where "pollinator gardens as nectar stopovers" should be developed, and thus encourage farmers to plant nectar sources in out-of-use areas (Withgott 1999).

GPM - Global Phenological Monitoring

This program is an initiative of the International Society of Biometeorology. It aims to link phenological networks around the world in order to assess climatic change effects using a variety of tools, including specially designed GPM-gardens with selected species. The core website is at http://www.dow.wau.nl/msa/gpm/.

Introduction of pollination parameters in restoration practices

The INESP (International Network of Expertise for Sustainable Pollination) and the NAPPC (the North American Pollinator Protection Campaign) in Costa Rica have proposed that standard recovery plans should include a study of whether the restoration program has restored the pollinator community at the field site. By constructing webs describing the plant-pollinator interactions at pristine sites, a picture of a healthy pollinator system will be obtained. This can be used as a reference when studying plots in restored systems. Without the restoration of the pollination system, the restoration program is not sustainable. More information is available at http://www.nappc.org.

ALARM

ALARM (*Assessing LArge-scale environmental Risks with tested Methods*, EC Framework 6 Integrated Project 2004-2009) is a large European project which assesses changes in continental biodiversity. It includes a specific pollination module whose main objectives are to: a) quantify distribution shifts in key pollinator groups (to provide continental-scale evidence for pollinator declines); b) measure the biodiversity and economic risks associated with loss of pollination services; c) determine the relative importance of the triggers of pollination loss (land use, climate change, environmental chemicals, invasive species and socio-economic factors) and d) develop predictive models for pollinator loss and consequent risks (Potts & Roberts 2004). It is expected that ALARM will increase its scientific and technical knowledge before application of the announced European Pollinator Initiative, which is open to interested researchers (www.European PollinatorInitiative.org). The similar projects, currently being developed in Africa, are available at: www.scienceinafrica.co.za/pollinator.htm.

This non-exhaustive review highlights the extent of the endangered status of pollination mutualisms. On the basis of the data available, we conclude that further research to assess pollination declines and their related mechanisms is required and that conservation programs should be implemented at local and large scales.

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