

Pollen and seed dispersal among dispersed plants

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ABSTRACT

The ecological significance of spacing among plants in contributing to the maintenance of species richness, particularly in tropical forests, has received considerable attention that has largely focussed on distance- and density-dependent seed and seedling mortality. More recently it has become apparent that plant spacing is also relevant to pollination, which often constrains seed production. While seed and seedling survival is reduced at high conspecific densities, pollination success, by contrast, is positively correlated to local conspecific density. Distance-dependent mechanisms acting on pollination and seed production have now been described for a variety of plants, with relatively isolated plants or fragmented populations generally suffering reduced fecundity due to pollen limitation. Yet there is considerable variability in the vulnerability of plant species to pollination failure, which may be a function of breeding system, life history, the pollination vector, the degree of specialisation among plants and their pollinators, and other indirect effects of habitat change acting on plants or pollinators. As reduced tree densities and population fragmentation are common outcomes of anthropogenically altered landscapes, understanding how pollination processes are affected in such degraded landscapes can inform effective conservation and management of remaining natural areas.

Key words: Allee effects, density, fragmentation, invasive species, mutualisms, pollination, seed dispersal, seed production, reproductive success.

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I. INTRODUCTION

You ever notice that trees do everything to get attention we do, except walk? (Alice Walker, *The Color Purple*)

Trees don't walk. They are rooted to the spot where they depend on agents of pollen and seed dispersal for successful sexual reproduction. Consequently, their flower and fruit displays have evolved to attract pollinators and seed dispersers from a distance. But are plants sufficiently attractive to overcome distances between neighbours in our modern human-dominated landscapes? This question has generated considerable research interest, not least because of its relevance to the viability and conservation of populations and species in disturbed landscapes.

Recent decades have witnessed dramatic impacts of human land use in both temperate and tropical regions that have changed the distribution of natural habitats and the relative abundance of the species they contain. Logging and clearance of natural vegetation for agriculture and development has caused degradation of forests and other habitats through the partial removal of economically important species or fragmentation and isolation of remnant habitat patches. Media attention has been focussed on the clearance and fragmentation of tropical forests, but of course other habitats and species have been subject to similar impacts. In temperate zones heathlands and native grasslands have been fragmented and greatly reduced in area. Exacerbating these impacts is the rapid spread of plants that have been accidentally or deliberately introduced into novel environments. Despite efforts to limit further changes in land cover and restrict the spread of invasives it seems certain that future generations will be living within landscapes very different to those of only 50 years ago. In temperate regions we have already become accustomed to fragmented natural habitats in human-dominated landscapes, and our nature reserves and protected area systems aim to preserve the best of what is left. In the tropics the process of fragmentation and degradation of natural areas continues more or less unabated, and even today's landscapes are likely to be wistful memories for tomorrow's generation.

Changes in the distribution of habitats across landscapes are paralleled by local dynamics of species turnover. Plants and animals become locally extinct in small fragments in response to altered microclimates, edge effects, insufficient habitat to support a home range, increased susceptibility to catastrophic events, inbreeding and other reasons. Plants that are dependent on mutualistic partners to ensure reproductive success have an additional problem: rapid changes in landscape pattern, local densities, and/or the

sudden appearance of novel invasive species, may cause shifts in the behaviour or abundance of mutualists involved in plant reproductive processes. Comparatively rapid isolation of plant populations, coupled with lowered local densities of individuals within populations, has already been shown to cause a decline in individual reproductive output for plant species from several habitats (see Table 1 for examples and references). Where such reproductive decline is substantial populations may become locally extinct through insufficient recruitment. Such changes may not be immediately obvious owing to the inherent time lags introduced by long plant life-spans.

In this review I explore the extent to which, and by what mechanisms, recent changes to the spatial distribution of vascular plants impact their reproduction by seed in recently altered landscapes. I begin by identifying the components of plant spatial distributions, namely local density, relative abundance and population fragmentation, that are relevant to this discussion. Not all plants are expected to be equally vulnerable to such changes, and I briefly consider the characteristics and conditions that make them so. Thereafter, spatial effects on pollination and seed dispersal are discussed from both ecological and, to a lesser extent, genetic perspectives. The basic premise is that as individuals become increasingly isolated reproductive processes, such as pollination and seed dispersal, begin to function less efficiently leading to Allee effects whereby declining population density or abundance results in a disproportionate decline in reproductive output and population viability. The relevance of this to conservation is obvious – many isolated or depauperate plant populations, particularly in tropical regions, may cease to be reproductively viable, or may be exposed to greater extinction risk owing to reduced reproductive capacity, particularly when threats are compounded by invasive species or changing climate.

II. SPATIAL DIMENSIONS OF PLANT DISTRIBUTIONS

The distribution of individuals and populations across a landscape can be described by several attributes, each of which gives only a partial picture of spatial complexity (Fig. 1). Although values for density, fragmentation, areal cover, relative frequency and population size may be closely correlated, it is nevertheless important not to confound them as the mechanisms through which they affect plant reproduction are likely to differ. Indeed, spatial distributions can only be realistically represented by combined use of multiple

interrelated dimensions, and in discussing ecological interactions in relation to spatial parameters it is necessary to identify exactly what dimensions are being invoked. For example, habitat fragmentation reduces population size, but local population density within resulting subpopulations may remain largely unaffected, while isolation of subpopulations is a non-linear function of area cover (Andren, 1994; With & Crist, 1995; With, Gardner & Turner, 1997). Thus Allee effects may imply either low population size, low population density, or both. Even where population size and distribution remain unaffected, relative abundance may vary depending on the nature of the surrounding vegetation.

(1) Fragmentation

Fragmentation refers to the division of a continuous habitat and can be applied to any scale over which continuity is relevant to ecosystem functioning. Fragmentation is distinguished from population size in that it implies the combination of two spatial elements, fragment size *and* fragment isolation, whereas population size simply refers to the number of individuals in a predefined patch. Patch area is frequently recorded as a surrogate for population size, but population size is not always correlated with patch size (see for example Donaldson *et al.*, 2002). Interrelated attributes of fragments include isolation, size and boundary characteristics of patches, all of which are related to the extent of fragmentation, while fragment density, or aggregation, is likely to moderate the degree of difference between the patches and surrounding matrix (Lord & Norton, 1990). The abundance and behaviour of animal vectors of plant gene flow are likely to be affected by each of these attributes. They are also likely to be affected by the scale of fragmentation: at coarse resolution across a landscape a large continuous area is divided into several smaller and more or less isolated intact habitat 'islands', while at the other extreme vegetation may become fragmented by the invasion of alien species thereby reducing local purity. Here I use 'fragmentation' to refer to the pattern of habitat distribution at landscape scales and reserve the term 'purity' for examples of finer scale fragmentation (see below).

Landscape connectivity is especially important in facilitating movement of pollinators or seed dispersers across a fragmented landscape (Jonsen & Fahrig, 1997; Santos, Telleria & Virgos, 1999), and is a non-linear function of the extent of fragmentation (Andren, 1994; With & Crist, 1995; With *et al.*, 1997). In the early stages of fragmentation connectivity remains high and changes little allowing animal movement across a fragmented landscape largely within the original habitat matrix. With increasing fragmentation a threshold is reached where habitat islands begin to be created forcing animals to cross habitat boundaries when moving across the landscape. Connectivity declines rapidly at this stage until most of the landscape consists of habitat islands after which subsequent marginal decline of connectivity with continued clearance is low. Hence area and isolation effects may influence the population size or behaviour of pollinator or seed disperser mutualists to differing degrees depending on the proportion of habitat cleared, and the pattern by which it has been cleared. Andren (1994) has

shown for birds that where more than 30% of suitable habitat remains the effects of fragmentation can be attributed mainly to habitat loss, while in highly fragmented landscapes patch size and isolation add to the effects of habitat loss leading to more pronounced effects than would be expected by area alone. Thus rapid changes in the size and isolation of patches occur at certain threshold values for the proportion of habitat remaining in the landscape, and radical changes in the movement of animals between patches may result at these threshold states (see for example Lennartsson, 2002). Ecological processes that depend on movement of individuals across a landscape may be vulnerable to sudden changes in their functioning as these thresholds are crossed.

(2) Density and distance between neighbours

At smaller scales changes in density may take place within a habitat which remains otherwise intact. In such situations it is simply the distance between neighbouring individuals that is the relevant parameter rather than the distance between subpopulations across an intervening and qualitatively different matrix. From an ecological perspective density becomes critical when the distance between conspecific neighbours leads to changes in the foraging behaviour of pollinators or seed dispersers. Distance effects on plant reproduction are mediated by the type of mutualist or, more specifically, the dispersal capabilities of these mutualistic partners. Flight capabilities remain poorly resolved for most pollinating agents, but where they have been quantified the results can be surprising. Tiny fig wasps have been shown to transfer pollen successfully between trees separated by over 10 km in tropical forest (Nason, Herre & Hamrick, 1998) and as much as 84 km along desert valleys (Ahmed, 2003). With such long-distance pollen dispersal by even the weakest of insects it may seem that there should be little concern for reproductive decline through spatial isolation, and yet such pollen-limited reproductive decline has been demonstrated for a variety of plants (Burd, 1994; Larson & Barrett, 2000). This, in part, is probably because pollinators move only a fraction of the distances that they are capable of. Thus bumblebees may limit their foraging flights to an area of only a few square metres despite being able to move much further (Sowig, 1989; Smithson & Macnair, 1997*a*).

(3) Purity

Most flowering plants achieve pollination and seed dispersal by attracting animal vectors to resource-rich flowers or fruit. In most situations the animal vectors respond to plants according to their relative rather than absolute abundance, and plants often have to compete for pollinators and seed dispersers with their near neighbours. The proportional abundance of plants relative to all other flowering (or fruiting) plants in the local area may be an important determinant of reproductive success as many pollinators and seed dispersers respond to resource availability in a frequency-dependent manner (Smith *et al.*, 1989; Smithson & Macnair, 1996; Smithson & Macnair, 1997*a*). Thus,

Table 1. A summary of impacts of population size, density, purity and patch size (fragmentation) on plant reproductive ecology. BS refers to breeding system as self-compatible (C) or self-incompatible (I). E/O refers to the type of study as either experimental (E) or observational (O). Pollinators are listed when known. When information on breeding system or pollinators was not available in the source publication it was derived from elsewhere. Not significant correlations are shown in bold, and spatial variables that are negatively correlated with reproductive success (i.e. declining reproductive success at high population abundance, density, purity or large patch size) are italicised. Information on 123 species belonging to 59 families and from 84 studies is included.

Species	Family	BS	Life form	Cause	Response	Pollinator	E/O	Reference
<i>Lasiosiphon eriocephalus</i>	Thymeleaceae	C	Shrub	Density	No effect (pollinator visitation, seed set)	Beetles	O	Somanathan <i>et al.</i> (2004)
<i>Taxus canadensis</i>	Taxaceae	C	Coniferous shrub	Density	Seed set	Wind	O	Allison (1990)
<i>Nesohedytis arborea</i>	Rubiaceae	I	Dioecious tree	Density	Pollinator visitation, fruit set	Syrphid flies	O	Percy & Cronk (1997)
<i>Brosimum alicastrum</i>	Moraceae	Partially I	Gyno-dioecious tree	Density	No effect (outcrossing)	Small insects (& possibly wind)	O	Murawski & Hamrick (1991)
<i>Senecio integrifolius</i>	Asteraceae	I	Herb	Density	Seed set	Bees	O	Widen (1993)
<i>Senecio crassulus</i>	Asteraceae	C	Herb	Density	Pollen grains on stigma	Bees	O	Thomson (1981)
<i>Senecio integerrimus</i>	Asteraceae	C	Herb	Density	No effect (pollinator visits, fruit set, seeds per plant)	Bees & butterflies	E	Schmitt (1983 <i>a</i>)
<i>Senecio jacobaea</i>	Asteraceae	C	Herb	Density	Pollinator visitation; no effect (fruit set or seeds per plant)	Bees & flies	E	Kunin (1997)
<i>Echium vulgare</i>	Boraginaceae	C	Herb	Density	No effect (pollinator visits)	Bees	O	Klinkhamer & de Jong (1990)
<i>Silene uniflora</i>	Caryophyllaceae	C	Herb	Density	No effect (fruit and seed set)	Sphingid & noctuid moths	O	Pettersson (1997)
<i>Salvia pratensis</i>	Labiatae	C	Herb	Density	Outcrossing	Bumblebees	O, E	van Treuren <i>et al.</i> (1993)
<i>Cynoglossum officinale</i>	Boraginaceae	I	Herb	Density	Pollinator visitation	Bees	O	Klinkhamer <i>et al.</i> (1989)
<i>Diplotaxis erucoides</i>	Brassicaceae	I	Herb	Density	Fruit set; seed set per fruit; seed set per plant	Small bees & flies	O	Kunin (1992)
<i>Lesquerella fendleri</i>	Brassicaceae	I	Herb	Density	Seed set	Small bees	O	Roll <i>et al.</i> (1997)
<i>Brassica kaber</i>	Cruciferae	I	Herb	Density	Pollinator visits & pollination quality	Honeybees & syrphids	E	Kunin (1993)
<i>Palicourea</i> sp.	Rubiaceae	I	Herb	Density	Pollen grains on stigma & seeds per fruit	Hummingbirds	E	Feinsinger <i>et al.</i> (1991)
<i>Agalinis strictifolia</i>	Scrophulariaceae	I	Parasitic herb	Density	No effect (pollination)	Honeybees & bumblebees	O	Dieringer (1992)
<i>Cassia biflora</i>	Caesalpiniaceae		Shrub	Density	Pollinator visitation, seed set	Bees	O	Silander (1978)
<i>Astragalus canadensis</i>	Leguminosae	I	Shrub	Density	Fruit set	Bees	E	Platt <i>et al.</i> (1974)
<i>Besleria triflora</i>	Gesneriaceae	C	Shrub/small tree	Density	Pollen grains on stigma; no effect (seeds per fruit)	Hummingbirds	E	Feinsinger <i>et al.</i> (1991)
<i>Pachira quinata</i>	Bombacaceae		Tree	Density	Outcrossing	Bats	O	Fuchs <i>et al.</i> (2003)
<i>Cavanillesia platanifolia</i>	Bombacaceae	C	Tree	Density	Outcrossing	Hawkmoths, bees, hummingbirds,	O	Murawski <i>et al.</i> (1990)

<i>Thuja occidentalis</i>	Cupressaceae	C	Tree	Density	Outcrossing	Wind	O	Perry and Knowles (1990)
<i>Quercus douglasii</i>	Fagaceae	C	Tree	Density	Seed set	Wind	O	Knapp <i>et al.</i> (2001)
<i>Pinus contorta</i>	Pinaceae	C	Tree	Density	Seed set	Wind	O	Smith <i>et al.</i> (1988)
<i>Quararibea asterolepis</i>	Bombacaceae	I	Tree	Density	Outcrossing	Hawkmoths, bats, monkeys	O	Murawski & Hamrick (1991)
<i>Tachigali versicolor</i>	Fabaceae	I	Tree	Density	No effect (outcrossing)	Bees	O	Murawski & Hamrick (1991)
<i>Fagus sylvatica</i>	Fagaceae	I	Tree	Density	Seed set	Wind	O	Nilsson & Wastljung (1987)
<i>Beilschmiedia pendula</i>	Lauraceae	I	Tree	Density	No effect (outcrossing)	Small insects	O	Murawski & Hamrick (1991)
<i>Neolitsia dealbata</i>	Lauraceae	I	Tree	Density	Pollinator visitation; pollen dispersal; fruit set	Small generalist insects	O	House (1993)
<i>Trichilia turbeculata</i>	Meliaceae	I	Tree	Density	No effect (outcrossing)	Bees?	O	Murawski & Hamrick (1991)
<i>Sorocea affinis</i>	Moraceae	I	Tree	Density	No effect (outcrossing)	Small bees and wind	O	Murawski & Hamrick (1991)
<i>Ceiba pentandra</i>	Bombacaceae	Partially I	Tree	Density	Outcrossing	Bats, birds, bees, beetles	O	Murawski & Hamrick (1992)
<i>Pachira quinata</i>	Bombacaceae	Partially I	Tree	Density	Fruit set; no effect (seed per fruit)	Bats and sphingid moths	O	Fuchs <i>et al.</i> (2003)
<i>Shorea megistophylla</i>	Dipterocarpaceae	Partially I	Tree	Density	Outcrossing	Large bees (<i>Apis</i>)	O	Murawski <i>et al.</i> (1994)
<i>Shorea siamensis</i>	Dipterocarpaceae	Partially I	Tree	Density	Pollination, seed set	Small bees	O	Ghazoul <i>et al.</i> (1998)
<i>Platypodium elegans</i>	Fabaceae	Partially I	Tree	Density	No effect (outcrossing)	Small bees	O	Murawski & Hamrick (1991)
<i>Aristotelia chilensis</i>	Eleocarpaceae	I	Dioecious tree	Density and purity	No effect (pollinator visitation, pollination, pollen quality, fruit set, seed production)	Cadeguala albopilosa (colletid) and halictid bees	O	Vazquez & Simberloff (2004)
<i>Alstroemeria aurea</i>	Alstroemeriaceae	C	Herb	Density and purity	Pollen quality, fruit set, seed production (all show weak effects); no effect (pollinator visitation)	Diverse insects	O	Vazquez & Simberloff (2004)
<i>Ribes megellanicum</i>	Saxifragaceae	C	Shrub	Density and purity	No effect (pollinator visitation, pollination, pollen quality, fruit set)	Bees	O	Vazquez & Simberloff (2004)
<i>Cyanthum diemii</i>	Asclepiadaceae		Vine	Density and purity	No effect (pollinator visitation, pollination, pollen quality, fruit set, seed production)	Bees, parasitoids, ants	O	Vazquez & Simberloff (2004)
<i>Gerbera aurantiaca</i>	Asteraceae	I	Herb	Patch size	Pollination, seed production	Monkey beetles (Scarabaeidae: Hopliini)	O	Johnson <i>et al.</i> (2004)
<i>Tilandsia ixiodes</i>	Bromeliaceae	I	Epiphyte	Patch size	No effect (pollination, reproductive success)	Hummingbirds	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Rhipsalis lumbricoides</i>	Cactaceae	I	Epiphyte	Patch size	Pollination, reproductive success	Butterflies, bees, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)

Table 1. (cont.)

Species	Family	BS	Life form	Cause	Response	Pollinator	E/O	Reference
<i>Ligaria cuneifolia</i>	Loranthaceae	C	Hemi-parasite	Patch size	Pollination (<i>—ve effect</i>); no effect (reproductive success)	Hummingbirds	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Berkheya armata</i>	Asteraceae		Herb	Patch size	No effect (fruit set)	Diverse small insects	O	Donaldson <i>et al.</i> (2002)
<i>Gladiolus liliaceus</i>	Iridaceae		Herb	Patch size	No effect (fruit set)	Noctuid moths	O	Donaldson <i>et al.</i> (2002)
<i>Pterogydium catholicum</i>	Orchidaceae		Herb	Patch size	Fruit set (lack of pollinators)	<i>Rediviva</i> spp. bees	O	Donaldson <i>et al.</i> (2002)
<i>Dianella revolute</i>	Phormiaceae		Herb	Patch size	Reproductive success	Large bees	O	Cunningham (2000 <i>b</i>)
<i>Cyanella lutea</i>	Tecophilaeaceae		Herb	Patch size	No effect (fruit set)	Large bees	O	Donaldson <i>et al.</i> (2002)
<i>Justicia squarrosa</i>	Acanthaceae	C	Herb	Patch size	Pollination, reproductive success	Butterflies	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Campanula cervicaria</i>	Campanulaceae	C	Herb	Patch size	No effect (reproductive success)	Bees, flies	O	Eisto <i>et al.</i> (2000)
<i>Dianthus deltoides</i>	Caryophyllaceae	C	Herb	Patch size	Pollination, seed set	Butterflies	O	Jennersten (1988)
<i>Lychnis viscaria</i>	Caryophyllaceae	C	Herb	Patch size	Pollination; no effect (reproductive success)	Bees, butterflies, flies	E	Mustajärvi <i>et al.</i> (2001)
<i>Viscaria vulgaris</i>	Caryophyllaceae	C	Herb	Patch size	Seed set	Bumblebees and butterflies	O	Jennersten and Nilsson (1993)
<i>Gentianella campestris</i>	Gentianaceae	C	Herb	Patch size	Seed set	Bumblebees	O	Lennartsson (2002)
<i>Gentianella germanica</i>	Gentianaceae	C	Herb	Patch size	Reproductive success	Flies, bees	O	Fischer & Matthies (1998)
<i>Ornithogalum thyrsoides</i>	Hyacinthaceae	C	Herb	Patch size	No effect (fruit set)	Bees and beetles	O	Donaldson <i>et al.</i> (2002)
<i>Betonica officinalis</i>	Lamiaceae	C	Herb	Patch size	Pollinator visitation, increased visitation time per patch, outcrossing	Bumblebees	E	Goverde <i>et al.</i> (2002)
<i>Portulaca umbraticola</i>	Portulacaceae	C	Herb	Patch size	Pollination, reproductive success	Small bees, butterflies	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Trachyandra hirsuta</i>	Asphodelaceae	I	Herb	Patch size	No effect (fruit set)	Beetles, bees, flies	O	Donaldson <i>et al.</i> (2002)
<i>Eupatorium perfoliatum</i>	Asteraceae	I	Herb	Patch size	No effect (reproductive success)	Wasps, bees, flies, moths	O	Byers (1995)
<i>Eupatorium resinosum</i>	Asteraceae	I	Herb	Patch size	Reproductive success	Wasps, bees, flies, moths	O	Byers (1995)
<i>Calystegia collina</i>	Convolvulaceae	I	Herb	Patch size	Seed set	Bees	O	Wolf & Harrison (2001)
<i>Raphanus sativus</i>	Cruciferae	I	Herb	Patch size	Pollination, reproductive success	Solitary bees	O	Steffan-Dewenter & Tscharnkte (1999)
<i>Sinapis arvensis</i>	Cruciferae	I	Herb	Patch size	Pollination, reproductive success	Bees, flies, beetles, wasps, bugs	O	Steffan-Dewenter & Tscharnkte (1999)
<i>Babiana ambigua</i>	Iridaceae	I	Herb	Patch size	<i>Fruit set (—ve effect)</i>	Diverse small insects	O	Donaldson <i>et al.</i> (2002)
<i>Trillium ovatum</i>	Liliaceae	I	Herb	Patch size	No effect (reproductive success)	Beetles, bees, moths	O	Jules & Rathcke (1999)
<i>Oenothera macrocarpa</i>	Onagraceae	I	Herb	Patch size	Pollination, reproductive success	Hawkmoths	O	Moody-Weis & Heywood (2001)
<i>Ipomopsis aggregate</i>	Polemoniaceae	I	Herb	Patch size	Pollination, reproductive success	Hummingbirds	O	Heschel & Paige (1995)
<i>Primula elatior</i>	Primulaceae	I	Herb	Patch size	Reproductive success	Bees, other insects	O	Jacquemyn <i>et al.</i> (2002)
<i>Calyptrogyne ghiesbreghtiana</i>	Palmaceae		Palm	Patch size	Pollen load	Bats	O	Cunningham (1996)

<i>Astroloma conostephioides</i>	Epacridaceae		Shrub	Patch size	Fruit set	Birds	O	Paton (2000)
<i>Acacia brachybotrya</i>	Fabaceae		Shrub	Patch size	Pollination, fruit set	Diverse insects	O	Cunningham (2000 <i>a</i>)
<i>Senna artemisioides</i>	Fabaceae		Shrub	Patch size	<i>Reproductive success</i> (— <i>ve effect</i>)	Large bees	O	Cunningham (2000 <i>b</i>)
<i>Cassia aphylla</i>	Fabaceae	C	Shrub	Patch size	Pollination; no effect (reproductive success)	Large bees	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Mimosa detinens</i>	Fabaceae	C	Shrub	Patch size	Reproductive success; no effect (pollination)	Moths, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Atamisquea emarginata</i>	Capparaceae	I	Shrub	Patch size	Pollination, reproductive success	Bees, wasps, moths	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Acacia furcatispina</i>	Fabaceae	I	Shrub	Patch size	<i>Reproductive success</i> (— <i>ve effect</i>); no effect (pollination)	Butterflies, bees, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Caesalpinia gilliesii</i>	Fabaceae	Partially I	Shrub	Patch size	Pollination; no effect (reproductive success)	Hawkmoths	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Opuntia quimilo</i>	Cactaceae	I	Succulent	Patch size	No effect (pollination, reproductive success)	Medium-large bees	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Opuntia stricta</i>	Cactaceae	I	Succulent	Patch size	Pollination, reproductive success	Bees	O	Spears (1987)
<i>Eremophila glabra</i>	Myoporaceae		Tree	Patch size	Pollination, fruit set	Birds	O	Cunningham (2000 <i>a</i>)
<i>Dimizia excelsa</i>	Fabaceae	C	Tree	Patch size	Increased selfing; larger genetic neighbourhoods	Exotic honeybees	O	Dick <i>et al.</i> (2003)
<i>Symphonia globulifera</i>	Guttiferae	C	Tree	Patch size	Pollination, <i>reproductive output</i> (— <i>ve effect</i>); <i>outcrossing</i> (— <i>ve effect</i>)	Hummingbirds, birds	O	Aldrich & Hamrick (1998)
<i>Spondias mombin</i>	Anacardiaceae	I	Tree	Patch size	Pollination, reproductive success	Small diverse insects	O	Nason & Hamrick (1997)
<i>Ceiba grandiflora</i>	Bombacaceae	I	Tree	Patch size	Pollination, fruit set	Bats	O	Quesada <i>et al.</i> (2003)
<i>Acacia aroma</i>	Fabaceae	I	Tree	Patch size	Pollination, reproductive success	Medium-large bees	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Acacia atramantaria</i>	Fabaceae	I	Tree	Patch size	<i>Reproductive success</i> (— <i>ve effect</i>); no effect (pollination)	Bees, beetles	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Acacia praecox</i>	Fabaceae	I	Tree	Patch size	No effect (pollination, reproductive success)	Bees, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Cercidium australe</i>	Fabaceae	I	Tree	Patch size	Pollination; no effect (reproductive success)	Bees, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Prosopis nigra</i>	Fabaceae	I	Tree	Patch size	Pollination, reproductive success	Bees, flies, wasps	O	Aizen & Feinsinger (1994 <i>a</i>)
<i>Pithecellobium elegans</i>	Mimosoideae	I	Tree	Patch size	Genetic diversity; fruit set	Hawkmoths	O	Hall, Walker & Bawa (1996)
<i>Embothrium coccineum</i>	Proteaceae	I	Tree	Patch size	<i>Pollination</i> (— <i>ve effect</i>)	Birds, hummingbirds	O	Smith-Ramírez & Armesto (2003)
<i>Anacardium excelsum</i>	Anacardiaceae	Partially I	Tree	Patch size	Seed set; no effect (pollination)	Small bees, flies	O	Ghazoul & McLeish (2001)
<i>Centrosema virginianum</i>	Fabaceae	C	Vine	Patch size	Pollination, reproductive success	Large bees	O	Spears (1987)

Table 1. (*cont.*)

Species	Family	BS	Life form	Cause	Response	Pollinator	E/O	Reference
<i>Clarkia concinna</i>	Onagraceae	C	Herb	Patch size & density	Pollination, seed set	Bees, butterflies & flies	E	Groom (1998)
<i>Nepeta cataria</i>	Labiatae	C	Herb	Patch size & isolation	Pollinator visitation	Bees	O	Sih & Baltus (1987)
<i>Samanea saman</i>	Leguminosae	I	Tree	Patch size & isolation	Outcrossing, seedling vigour	Sphingid moths	O	Cascante <i>et al.</i> (2002)
<i>Lupinus sulphureus</i>	Fabaceae	I	Herb	Patch size, density, population size	Fruit set, inbreeding depression	Bumblebees, solitary bees	O	Severns (2003)
<i>Babiana ambigua</i>	Iridaceae	I	Herb	Pollinator diversity	Fruit set	Diverse small insects	O	Donaldson <i>et al.</i> (2002)
<i>Heterophragma quadriloculare</i>	Bignoniaceae	I	Tree	Population size	No effect (pollinator visitation, seed set)	Carpenter bees	O	Somanathan <i>et al.</i> (2004)
<i>Panax quinquefolius</i>	Araliaceae	C	Herb	Population size		Halictid bees and syrphid flies	E	Hackney & McGraw (2001)
<i>Silene regia</i>	Caryophyllaceae	C	Herb	Population size	Outcrossing	Hummingbirds	O	Menges (1991)
<i>Stellaria pubera</i>	Caryophyllaceae	C	Herb	Population size	Pollination ; no effect (seeds per fruit)	Bees & flies	E	Campbell (1985)
<i>Succisa pratensis</i>	Dipsacaceae	C	Herb	Population size	Seed set; seed viability	Insects	O	Vergeer <i>et al.</i> (2003)
<i>Ornithogalum thyrsoides</i>	Hyacinthaceae	C	Herb	Population size	Seeds per fruit	Bees and beetles	O	Donaldson <i>et al.</i> (2002)
<i>Salvia pratensis</i>	Labiatae	C	Herb	Population size	No effect (outcrossing)	Bumblebees	O, E	van Treuren <i>et al.</i> (1993)
<i>Argyroxiphium sandwicense</i>	Asteraceae	I	Herb	Population size	Seed set	Bees	O	Forsyth (2003)
<i>Arnica montana</i>	Asteraceae	I	Herb	Population size	Seed set, seedling size, number of flowering stems	Syrphid flies	O	Luijten <i>et al.</i> (2000)
<i>Leucochrysum albicans</i>	Asteraceae	I	Herb	Population size	No effect (seed production, seed viability)	Small insects	O	Costin <i>et al.</i> (2001)
<i>Rutidosia leptorrhynchoides</i>	Asteraceae	I	Herb	Population size	Seed set	Beetles, flies, moths	O	Morgan (1999)
<i>Brassica kaber</i>	Cruciferae	I	Herb	Population size	No effect (pollinator visitation, seed set)	Honeybees & syrphids	E	Kunin (1997)
<i>Babiana ambigua</i>	Iridaceae	I	Herb	Population size		Diverse small insects	O	Donaldson <i>et al.</i> (2002)
<i>Lythrum salicaria</i>	Lythraceae	I	Herb	Population size	Seed production per flower & per plant	Bumblebees	O	Ågren (1996)
<i>Anacamptis pyramidalis</i>	Orchidaceae	I	Herb	Population size	Pollinia removal (pollinator visitation)	Butterflies	O	Fritz & Nilsson (1994)

<i>Calypso bulbosa</i>	Orchidaceae	I	Herb	Population size	Pollen export (–ve effect)	Bumblebees	O	Alexandersson & Ågren (1996)
<i>Epipactis helleborine</i>	Orchidaceae	I	Herb	Population size	Pollinia removal (pollinator visitation)	Vespid wasps	O	Ehlers, Olesen & Ågren (2002)
<i>Orchis palustris</i>	Orchidaceae	I	Herb	Population size	Pollinia removal (pollinator visitation)	Bumblebees	O	Fritz & Nilsson (1994)
<i>Orchis spitzelii</i>	Orchidaceae	I	Herb	Population size	Pollinia removal (pollinator visitation)	Bumblebees	O	Fritz & Nilsson (1994)
<i>Phlox pilosa</i>	Polemoniaceae	I	Herb	Population size	Pollen deposition on stigmas	Butterflies	O	Hendrix & Kyhl (2000)
<i>Banksia goodii</i>	Proteaceae	I	Shrub	Population size	Total population seed production	Honey-possums & birds	O	Lamont <i>et al.</i> (1993)
<i>Primula elatior</i>	Primulaceae	I	Herb	Population size & isolation	Seed set; high fruit abortion at high density	Bumblebees & flies	O	Van Rossum <i>et al.</i> (2002)
<i>Stachys palustris</i>	Labiatae		Herb	Purity	Pollinator visitation, seed set	Bumblebees	E	Chittka & Schurkens (2001)
<i>Ipomoea purpurea</i>	Polemoniaceae	C	Herb	Purity	Outcrossing rate	Bumblebees	O	Epperson & Clegg (1987)
<i>Potentilla gracilis</i>	Rosaceae	C	Herb	Purity	Pollinator visitation (–ve effect)	Bees & flies	O	Thomson (1981)
<i>Senecio crassulus</i>	Asteraceae	C	Herb	Purity	Pollinator visitation (–ve effect)	Bees	O	Thomson (1981)
<i>Stellaria pubera</i>	Caryophyllaceae	C	Herb	Purity	Pollinator visitation; pollination quality; fruit set	Bees & flies	E	Campbell (1985); Campbell & Motten (1985)
<i>Brassica kaber</i>	Cruciferae	I	Herb	Purity	Pollination quality, seed set; no effect (pollinator visitation)	Honeybees & syrphids	E	Kunin (1993)
<i>Dipterocarpus obtusifolius</i>	Dipterocarpaceae	I	Tree	Purity	Pollinator visits & pollination quality; no effect (seed set)	Butterflies, moths, birds	O	Ghazoul (2002a, 2004)
<i>Lythrum alatum</i>	Lythraceae	I	Herb	Purity	Pollinator visitation, seed set	Honeybees & bumblebees	E	Brown <i>et al.</i> (2002)
<i>Phlox pilosa</i>	Polemoniaceae	I	Herb	Purity	Seed set	Butterflies		Levin (1972)
<i>Delphinium nuttallianum</i>	Ranunculaceae	I	Herb	Purity	Pollination, seed set	Bumblebees & hummingbirds	E	Schulke & Waser (2001)
<i>Palicourea lasiorrachis</i>	Rubiaceae	I	Herb	Purity	Pollinator constancy, pollen grains on stigma, fruit set; no effect (pollinator visitation)	Hummingbirds	E	Feinsinger <i>et al.</i> (1991)
<i>Besleria triflora</i>	Gesneriaceae	C	Shrub/Small tree	Purity	Seed set; no effect (pollinator visitation or pollination quality)	Hummingbirds	E	Feinsinger <i>et al.</i> (1991)

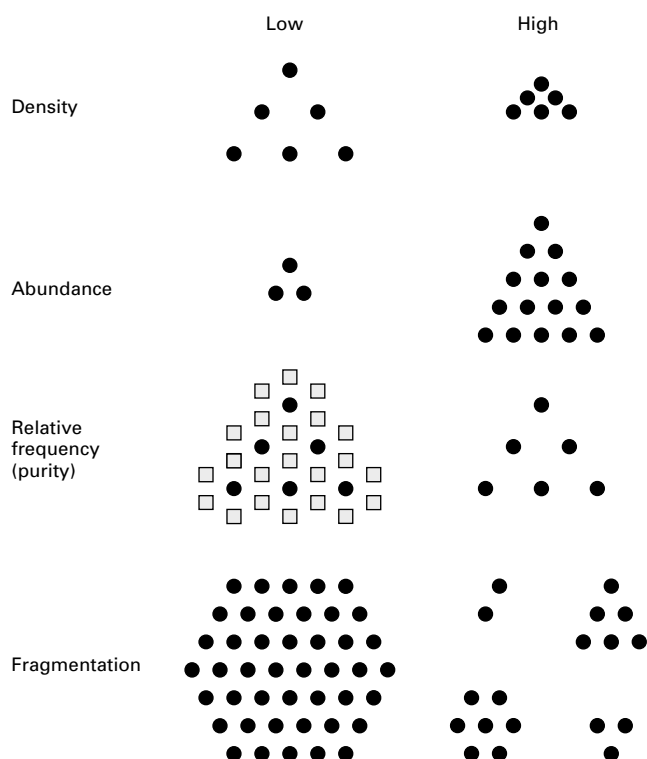


Fig. 1. Various dimensions of spatial patterns. Density refers to the spacing between neighbouring individuals; abundance is the size of a local population at a particular density; relative frequency, or purity, reflects the abundance of individuals relative to the abundance of individuals belonging to other species with respect some shared property; and fragmentation reflects the distance between recently formed subpopulations. Adapted from Kunin (1997).

invasive species, both alien and native, may alter the relative abundance of indigenous plants even if the latter's actual abundance and density remains unaffected. In determining relative abundance, more simply referred to as purity, we need to consider several spatial elements including aggregation or patchiness, individual size and the scale of observation: a single large isolated massively flowering tree may in itself represent 100% purity to poorly dispersing beetles, yet may contribute only a small proportion of the floral resources available to a wide-ranging bird or bat.

Changes in landscape pattern simultaneously affect multiple interrelated attributes simultaneously albeit not necessarily at equivalent rates, yet few studies clearly differentiate between them. Of course, in real landscapes it is usually difficult to isolate the effects of abundance, density, purity and fragmentation. Instead we rely on experimental approaches to disentangle these elements, and such work shows that the effects of plant size, density, purity and fragmentation on pollination and seed set do indeed differ qualitatively and quantitatively (Kunin, 1997). In general, however, all these factors have to a greater or lesser degree been implicated in the depression of plant reproductive output (Table 2).

Table 2. A summary of plant responses to density, population size, patch size (i.e. habitat fragmentation) and purity in terms of pollination (including pollinator visitation and pollen deposition) and reproductive success (as seed or fruit set). Figures refer to the number of studies in each category, with percentages provided in brackets. Studies that consider only the extent of outcrossing have been excluded. An 'effect' is determined as a significant positive correlation of the independent variable on pollination or reproductive output. 'No effect' refers to no association or a negative correlation between dependent and independent variables. Data are derived from Table 1 with exclusion of studies that show inconsistent results.

Spatial variable	Density	Population size	Patch size	Purity
Pollination				
Effect	12 (71)	6 (67)	28 (76)	6 (55)
No effect	5 (29)	3 (33)	9 (24)	5 (45)
Total	17	9	37	11
Reproductive output				
Effect	17 (65)	11 (79)	30 (59)	8 (89)
No effect	9 (35)	3 (21)	21 (41)	1 (11)
Total	26	14	51	9
Number of species	30	22	59	16
Number of studies	28	20	32	13

III. CHARACTERS THAT INCREASE VULNERABILITY TO ALLEE EFFECTS

Plants are not equal in how they respond to landscape changes. Life history, breeding system and phenological characteristics differentially affect vulnerabilities to Allee-related reproductive declines. Understanding which plant characteristics predispose species to Allee effects, and how they do so, will provide a basis by which we might begin to predict the effects of landscape changes on plant communities.

(1) Plant phenology

So far the landscape has been described in terms of plant distribution, yet it is the spatial and temporal coincidence of plant resources and mutualists that ultimately determines seed set. Plants only become 'accessible' to pollinators and seed dispersers when they bear flowers or fruit. Flowering and fruiting phenology is therefore central to our understanding of how changing plant distributions affect their reproduction. The timing, duration and intensity of flowering or fruiting can contribute to the likelihood of pollinator loss or the vulnerability of plants to such loss. Individual plants in a population may flower synchronously or asynchronously resulting in marked differences in effective population sizes (see Bronstein, 1995). The duration of flowering periods of both individuals and populations may be important for the persistence of mutualists particularly when flowering is asynchronous and unpredictable.

Plant phenology is also relevant at smaller scales. Competition for pollinators among individuals of synchronously and mass-flowering species (such as many Bornean dipterocarps) is likely to be high. Furthermore, mass-flowering species may attract many pollinators but the quality of pollinator visits may be low if the pollinators rarely move between trees (Frankie, Opler & Bawa, 1976). At the other extreme, an extended flowering period offers opportunities for many different flower visitors and reduces risks due to the loss of some pollinator taxa. *Lavandula latifolia* in southern Spain, for example, produces flowers for four months from July and is visited by more than 70 species of bees, flies, butterflies and moths (Herrera, 1987, 1988).

Bronstein (1995) described several types of plant-pollinator landscapes based on flowering phenologies and pollinator specialisation. Plants coupled with highly specialised pollinators may flower synchronously with flowering periods being timed to match pollinator occurrence (e.g. yuccas), or asynchronously, providing resources to pollinators more or less continuously (e.g. figs). In both these cases changes in phenological patterns may have severe impacts on pollinator viability, but changes to plant distributions are only likely to impact the latter. Most commonly, plants are visited by generalist pollinators and it makes little difference to pollinator persistence, at least on large scales, whether flowering of any one plant species is synchronous or asynchronous. Nevertheless, competition among plants for pollinators and the quality of pollinator visits may be temporarily influenced by local synchronous flowering events which swamp the floral market with a single floral currency.

(2) Specificity of reproductive mutualisms

Concern for plant reproductive systems in tropical environments has been emphasised owing to a perceived high degree of specialisation of plant-pollinator mutualisms (Bawa, 1990; Kearns, Inouye & Waser, 1998), although recent studies indicate that this may only be a marginal trend (Olesen & Jordano, 2002; Ollerton & Cranmer, 2002). Plants pollinated exclusively by a few specialist pollinator species are less vulnerable to poor or variable pollen quality, but instead risk pollinator decline at low density with little prospect of compensatory rescue (Bond, 1994). Communities with a high proportion of specialised interactions are therefore expected to be most susceptible to Allee effects. However, such plants may have other compensatory reproductive mechanisms such as clonal growth or independent selfing. Indeed it may be misleading to consider single traits in isolation as most plants have a suite of reproductive characteristics that, overall, may make them more or less equally resistant to the effects of disturbance, fragmentation and pollinator loss (Bond, 1994; Jules & Rathcke, 1999). In addition to compensatory reproductive mechanisms, both partners in specialised plant-pollination mutualisms tend to be reliably abundant over space and time (Waser *et al.*, 1996) possibly because, as Bond (1994) argues, extinction has already eliminated specialist partners that are not.

In a comparison of fragmentation-related reproductive changes among specialised and generalist pollination systems (including 46 species from 40 genera), Aizen, Ashworth &

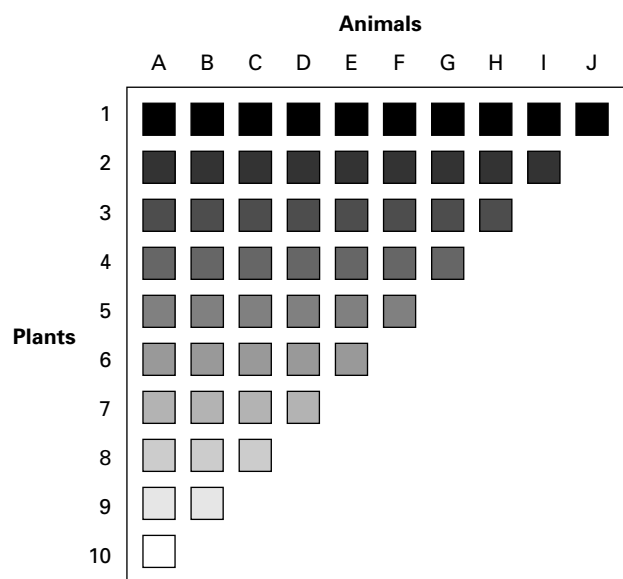


Fig. 2. A nested mutualistic network where ten plant species (1–10) are visited by one or more of ten animal partners (A–J). The partnerships are asymmetric in that the animal partners of specialist plants (such as plants 9 and 10) are themselves generalists and are sustained by many other plant species, and *vice versa*. Such nestedness appears common in pollinator and seed disperser networks and provides protection against perturbations (see text for details). However, compartmentalisation may, theoretically, arise within this nested structure if one or a few plants are considerably more abundant than others and if foraging decisions are frequency-dependent. In the figure, plant abundance is represented by the degree of shading, so under conditions of frequency-dependent foraging plant 1 attracts most of the pollinators including most visits by animal A which is the only species to visit plant 10. In such cases plant 10 not only suffers a reduction in visitation frequency, but also a decline in pollen quality with increased deposition of interspecific pollen on its stigmas. Frequency-dependent foraging may therefore undermine the buffering capacity of nested interaction networks. Figure adapted from Bascompte *et al.* (2003).

Galetto, 2002) concluded that there was no evidence to support the hypothesis that pollination specialisation increases the risk of plant extinction through declining reproductive seed set. Indeed, to assess properly the vulnerability of plants that have relatively specialised plant-pollinator (or seed disperser) mutualisms both sides of the interaction should be considered (Ashworth *et al.*, 2004). Specialisation among plants and pollinators is often assumed to be symmetrical – that is that specialist plants are pollinated by one or a few specialist pollinators while generalist plants are pollinated by a wide variety of generalist pollinators. In reality, it seems that asymmetric plant-animal interactions are more common (Bascompte *et al.*, 2003; Dupont, Hansen & Olesen, 2003; Vazquez & Aizen, 2004) resulting in highly nested pollinator and seed-disperser networks (Fig. 2; Bascompte *et al.*, 2003). Thus specialist plants tend to be visited by generalist animals, and specialist animals tend to visit plants that are also frequented by many other generalist partners (see also Ashworth *et al.*, 2004). Specialist pollinators that, by

definition, depend on a limited number of food sources, are more susceptible to habitat fragmentation than generalists that exploit a diverse array of alternative resources (Kunin, 1993; Bronstein, 1995). Nevertheless, because interactions tend to be asymmetric, loss of specialised pollinators impacts only generalist plants that are in any case buffered from such losses by the generalist pollinators that they also attract. Thereafter, further declines in the abundance of generalist pollinators would affect specialist and generalist plants equally. Asymmetric specialist-generalist interactions among plants and pollinators may therefore explain why specialist plants appear to be no more susceptible to fragmentation or other disturbances than generalist plants (Aizen *et al.*, 2002; Bascompte *et al.*, 2003). Furthermore, the distribution of interactions in highly nested mutualistic networks is centred on a core of generalist interactions to which all other interactions are connected (Bascompte *et al.*, 2003). Such a structure provides many alternative pathways that mutualistic processes may follow in the event of perturbation to part of the network, providing considerable resistance to perturbations for the network as a whole.

It is possible that plant-animal networks become more compartmentalised if animal mutualists visit plants in a frequency-dependent manner. Thus if the relative abundance of plant species in the community becomes increasingly polarised, for example if the community is invaded by a profusely flowering species, frequency dependent foraging by generalist pollinators or seed dispersers may result in disproportionate visitation to dominant species leaving rarer plants dependent on more specialist pollinators. Most pollinators are fairly catholic in the range of plants they visit (Herrera, 1988; Waser *et al.*, 1996) and, where plants are sparsely distributed in highly diverse communities, are more likely to behave as generalists. In such circumstances pollen quality, that is the proportion of pollen carried by a pollinator that is compatible with the plant being visited, is likely to be poor owing to the mix of species visited on successive flights. Low seed set has been linked to mixed pollen loads and stigma clogging by incompatible pollen types (Kunin, 1993). However, high connectivity in plant-animal mutualistic networks reduces vulnerability to Allee effects by providing alternative pathways by which ecological processes such as pollination and seed dispersal may be effected. Thus native pollinators that cease to become effective agents of pollen transfer may be replaced by introduced pollinators, such as African honeybees *Apis mellifera* in Amazonian forests (Dick, Etchelecu & Austerlitz, 2003) or European honeybees in Australia (Paton, 2000), that maintain the pollination function, although not necessarily to the same degree of efficiency as before (Paton, 1993; Gross & Mackay, 1998; Celebrezze & Paton, 2004).

(3) Pollen limitation and self-incompatibility

Pollen-limited seed set is of central importance if spacing mechanisms acting through pollination are to affect fruit production. Bateman's principle (see Burd, 1994) states that production of offspring is predominantly limited by the availability of resources rather than mating opportunities. Applied to vascular plants, this principle predicts that fruit

production is limited by maternal resources rather than pollen transfer. Indeed resource limitation of seed production was until recently thought to be prevalent among flowering plants (Bawa & Beach, 1981), and there remains great uncertainty about the relative importance of resource *versus* pollen limitation of fruit production among plants, as very few studies have examined both these factors simultaneously. However, we now know that pollen-limited seed production is, at the very least, not uncommon, and there now exists an abundance of studies that demonstrate this by experimental pollen supplementation (see reviews by Bierzychudek, 1981; Burd, 1994; Larson & Barrett, 2000). Burd's (1994) survey found 62% of 258 flowering plant species to be pollen limited at least in some locations or times. Pollen-limited seed set has been recorded from plants in arctic (Alatalo & Molau, 2001; Elberling, 2001), temperate (Paton, 2000; Goodwillie, 2001; Moody-Weis & Heywood, 2001; Ehrlén, Kack & Ågren, 2002) and tropical regions (Johnson & Bond, 1997; Larson & Barrett, 2000; Aizen, 2001). Critics note that responses to short-term pollen supplementation fail to capture lifetime reproductive success which, they maintain, remains resource limited. Although population-wide declines in reproductive success due to reduced pollen transfer have now been recorded in a range of plant species and geographic localities, there remains uncertainty over whether pollen-availability limits lifetime fitness or is simply a short-lived phenomenon.

Some species are more predisposed to being pollen-limited than others. In a comparative study of pollen-limited plants Larson & Barrett (2000) concluded that woody and tropical plants are more likely to be pollinator limited than herbaceous and temperate ones, but only among self-incompatible species (presumably because of greater dependence on pollen transfer by pollinators). Most tropical trees are indeed self-incompatible (Bawa, 1974; Bawa *et al.*, 1985) and may be predisposed to pollen limitation. Larson & Barrett (2000) further suggest that herbaceous plants are less likely to be pollen limited on account of the size of their floral displays relative to woody plants – large displays attract more pollinators but visitation rates per flower may be lower – but this presumably depends on the size of the floral display at a scale relevant to pollinator behaviour. The mechanism responsible for the prevalence of pollen limitation across tropical and temperate species is uncertain, though tropical species do tend to occur at lower densities and may have greater dependence on specialised biotic pollinating agents than temperate species (but see Waser *et al.*, 1996, and above).

Generally, self-compatible species are unlikely to be pollen limited as pollination can still be achieved in the absence of other local pollen sources by geitonogamy, and for self-pollinating plants, even in the absence of pollinators. A review by Aizen *et al.* (2002) concluded that pollinator visits to self-compatible plants were no less likely to decline in response to habitat fragmentation than for self-incompatible plants. Self-compatible plants may still be pollen limited if a pollinating vector is required for pollination, and Aizen *et al.* (2002) point to the potential bias arising from the tendency for studies to be conducted on species with showy flowers that depend on pollinators for seed set regardless of their

breeding system. Self-compatible plants may also be pollen limited if there is a genetic cost associated with selfing. However, regularly selfed plants may not be as susceptible to reproductive difficulties associated with inbreeding owing to the low genetic load typical of such populations (deleterious alleles having been previously purged). For partially self-incompatible plants expression of deleterious alleles through inbreeding may be reflected in reduced seed set, seed viability or germination success (Epperson & Clegg, 1987; Lennartsson, 2002; Severns, 2003).

(4) Growth form, breeding system and longevity

Several features of plant life histories are relevant to reproduction including longevity, size and breeding frequency. Long-lived species tend to have higher genetic loads resulting in strong inbreeding depression which may explain why most woody plants are predominantly self-incompatible (Barrett, Harder & Worley, 1997). Long-lived plants also tend to be large and therefore susceptible to geitonogamy by virtue of their large floral displays, so the risk of inbreeding depression may favour the evolution of self-incompatibility mechanisms or dioecy (Barrett *et al.*, 1997). On the other hand, repeated opportunities for reproduction buffer plants against short-term reproductive decline. Annuals, by contrast, with only a single reproductive opportunity are far less likely to be self-incompatible and are more frequently associated with autogamy (Jaimes & Ramirez, 1999), presumably to provide insurance against failure of cross-pollination. Semelparous plants, also constrained by a single reproductive opportunity may, by the same token, be expected to have a high degree of self-compatibility. Indeed in one comparative study of plant life histories all of five semelparous, compared to only 20 of 47 (42%) iteroparous species, were self-compatible (data derived from Ehrlén & Lehtila, 2002). The probability of this occurring by chance assuming no difference in the frequency of self-compatibility among semelparous and iteroparous species is only 1.3%.

Increased selection for outcrossing among large long-lived plants is thought to underlie the marked association between plant form and breeding system, with self-incompatibility, monoecy and dioecy being more usually associated with woody trees (Murcia, 1996). Trees may be expected to be particularly vulnerable to negative fragmentation effects on reproduction due to a dependence on animal agents of pollen flow coupled with the low density at which most tropical trees occur (Murcia, 1996). A comparison across life forms of reproductive vulnerabilities to fragmentation showed, contrary to expectation, that pollination of herbaceous species was more likely to be negatively affected by fragmentation than that of trees (Aizen *et al.*, 2002) implying that compatibility systems are not important predictors of reproductive responses to fragmentation (see also Table 3).

Monoecy and dioecy provide for the functional isolation of the sexes but incur dependency on pollinator-mediated gene exchange, which may be why many dioecious species have reverted to pollination by the more predictable mechanism of wind. However, wind-transported pollen has a strongly leptokurtic distribution (Knapp, Goedde & Rice,

Table 3. Comparison of the distribution of species responses to plant spacing in terms of reproductive output, as fruit set or seed production, among self-compatible and incompatible plants. Percentage values given in brackets. Self-incompatible plants do not appear to be more susceptible to Allee effects than self-compatible plants (see text for details). Data are derived from Table 1.

	Compatible	Incompatible
Allee effect	18 (62)	40 (71)
No effect	12 (38)	16 (29)
Total	30	56

2001; Koenig & Ashley, 2003), and most wind-pollinated plants typically occur in low-diversity, high-density stands. This apparent dependence on high-density stands for effective wind-pollination may make such plants especially susceptible to increased spatial isolation.

Larger plants, both within and among species, also tend to have extended flowering periods which may enhance pollinator visitation and opportunities for outcrossing (Schmitt, 1983*b*). This may be important in populations where individual loss is borne disproportionately by the largest individuals, as occurs in fragmented tropical forests (Laurance *et al.*, 2000).

(5) Life-history characteristics and seed dispersal

Elements of plant life history are also relevant to seed dispersal in changing landscapes. Mean seed mass increases with the shadiness and, to a lesser extent, the dryness of the seedling habitat. The stature of the parent plant and timing of seed production in relation to the seasons may also contribute to seed size. Positive correlations between shadiness, tree size and seed size have been reported in both tropical and temperate communities (Foster & Janson, 1985; Waller, 1988). Seed size in turn is a good predictor of the mechanism of seed dispersal, the smallest seeds being effectively dispersed by wind while increasingly larger seeds rely on increasingly larger biotic agents, the motility and ubiquity of which is likely to be differentially affected by plant and habitat spatial distributions.

The phenology of seed production may also be relevant to the mechanism of seed dispersal and therefore the vulnerability of seed dispersal to changing landscapes. Many trees time fruit production to coincide with bird migration patterns (Noma & Yumoto, 1997; Parrish, 1997), and along the eastern North American coast fruiting phenology corresponds with bird migrations more closely than in the milder climates of southern North America where seed dispersal relies on resident over-wintering birds that also use alternative food sources such as insects (McCarty *et al.*, 2002). Changes in landscape patterns may therefore have greater impacts on the trees that rely on migratory birds for dispersal, as migrant stopovers are not guaranteed and migratory patterns may change in response to resource availability.

IV. SPATIAL DISTRIBUTION, POLLINATION AND SEED PRODUCTION

To predict accurately the functioning of plant reproductive systems in changing environments we need to understand the relationships among plant distributions and landscape patterns, pollinator cognition and behaviour, and the interactions of plants with each other and with their mutualistic (and antagonistic) partners within the framework of their own life histories. This ambitious task has already been hampered by confusion over the use and application of terms describing plant distribution patterns, so it is perhaps surprising that, for some scenarios at least, we can begin to identify and outline some emerging generalisations about plant reproductive responses to density, fragmentation, population size or patch isolation.

(1) Density and distance between neighbours

Models of pollinator foraging and empirical field studies indicate that reproductive success in self-incompatible plants is likely to be strongly correlated with local population density (Feinsinger, Tiebout & Young, 1991; Kunin, 1993; Kunin, 1997). These empirical studies are supported by field studies of shrubs and trees pollinated by agents as diverse as birds, bats, bees, flies and wind (Platt, Hill & Clark, 1974; Silander, 1978; Heithaus, Stashko & Anderson, 1982; Feinsinger *et al.*, 1986; Klinkhamer, de Jong & de Bruyn, 1989; Allison, 1990; Feinsinger *et al.*, 1991; Kunin, 1992; House, 1993; Roll *et al.*, 1997; Ghazoul, Liston & Boyle, 1998; Groom, 1998; Ghazoul & McLeish, 2001; Forsyth, 2003; Fuchs, Lobo & Quesada, 2003) and attributed principally to a decline in pollinator visitation frequency following changes in pollinator behaviour in low plant density conditions (Ghazoul *et al.*, 1998) or local depression of pollinator populations (Robertson *et al.*, 1999).

Theoretical and experimental studies predict that at low plant density pollinators will visit a higher proportion of flowers on each plant before moving to neighbouring plants (Beattie, 1979; Heinrich, 1979; Kunin, 1993; Kunin, 1997). Field studies tend to support this prediction (Bosch & Blas, 1994; Ghazoul *et al.*, 1998; Bosch & Waser, 1999; Schulke & Waser, 2001; but see below). For example, small *Trigona* spp. bees pollinating flowers of the dipterocarp tree *Shorea siamensis* in Thailand made frequent flights between neighbouring trees when distances between them were less than 30 m, but following timber extraction, whereupon distances between neighbouring flowering trees often exceeded 30 m, the bees spent much more time foraging within the canopy of a single tree (Ghazoul *et al.*, 1998). Such behaviour increases the likelihood of geitonogamy which, for *S. siamensis* as an outcrossed and pollen-limited species, reduces seed set. However, even self-compatible plants such as *Clarkia concinna*, have been shown to be susceptible to density-related pollination and seed set declines (Groom, 1998), though for *C. concinna* the effects were scale dependent and occurred only among small populations (up to 50 individuals). Among smaller plants the spatial scale over which reproductive output can be affected by distance (or density) can be as little

as 1 m, as in the small bee-pollinated desert mustard *Lesquerella fendleri* (Roll *et al.*, 1997).

Wind-pollinated species are also susceptible to density effects (Nilsson & Wastljung, 1987; Smith, Hamrick & Kramer, 1988; Allison, 1990; Perry & Knowles, 1990; Knapp *et al.*, 2001). Populations of *Taxus canadensis*, an evergreen coniferous shrub, thinned by browsing deer (resulting in average nearest neighbour distances of up to 3 m compared with less than 20 cm in high-density sites) produced less pollen and had lower levels of pollination success and seed set than larger higher density populations (Allison, 1990). Similarly, *Fagus sylvatica* at reduced densities produced fewer viable seed (Nilsson & Wastljung, 1987).

Reproductive decline associated with isolation might be expressed through reduced genetic variability and progeny fitness rather than seed set. Outcrossing as a function of density has been noted among herbs and shrubs (Valdeyron, Dommee & Vernet, 1977; Wolff, Friso & Vandamme, 1988; van Treuren *et al.*, 1993), coniferous trees (Farris & Mitton, 1984) and tropical trees (Murawski *et al.*, 1990; Murawski & Hamrick, 1991, 1992; Murawski, Gunatilleke & Bawa, 1994; Cascante *et al.*, 2002). Partially self-incompatible species may be particularly vulnerable to increased expression of genetic load following elevated incidence of selfing at low densities (Aizen & Feinsinger, 1994a; Ågren, 1996; Kunin, 1997). Reproductive output of isolated *Samanea saman* trees in Costa Rica, for example, was only slightly depressed compared to trees in large continuous populations, but the seeds were more inbred and seedling growth less vigorous (Cascante *et al.*, 2002). On the other hand, high plant densities (Ellstrand, 1992) or large floral displays (Ohashi & Yahara, 2001) can reduce gene flow as pollinators respond to locally abundant floral resources and curtail their flight distances.

Some authors have reported no reproductive disadvantage associated with isolation and distance between neighbours (Dieringer, 1992; Pettersson, 1997). Relatively isolated *Silene uniflora*, pollinated by sphingid and noctuid moths, produced as many fruits and seeds per flower as individuals growing in clumped groups (Pettersson, 1997). However, distances between plants were not recorded and isolation was assessed instead by the number of neighbours within 1 m of each plant. Thus 'isolated' plants may have been little more than 1 m from their nearest neighbours and well within the foraging range of the plants' pollinators. Similarly, Dieringer (1992) reported no relationship between density and seed production of *Agalini strictifolia*. In this case 'low'-density plots contained about five plants per square metre, which again is well within the foraging capabilities of its bumblebee and honeybee pollinators. On the other hand, no obvious explanation for the absence of an Allee effect among low-density populations of a small dioecious tree *Aristotelia chilensis*, a vine *Cyanchum diemii* and a shrub *Ribes megellanicum* in cattle-grazed/browsed and trampled woodland could be provided by Vazquez & Simberloff (2004), although pollen limitation and, for two species, breeding system were not ascertained.

Despite some examples to the contrary (Schmitt, 1983a; Klinkhamer & de Jong, 1990; Dieringer, 1992; Pettersson, 1997) the large majority of studies have documented

reduced seed set at low density mediated through inadequate pollen flow (Table 1). The exceptions, on the whole, prove to be species that are either self-compatible or pollinated by wide-ranging pollinators (Chase *et al.*, 1996), or the result of inappropriate scales of observation (Dieringer, 1992; Pettersson, 1997). For each species there is a continuum of plant densities some point along which pollination systems begin to break down. The point at which this happens is determined by a complex of factors, including the abundance and foraging ranges of pollinators, size of the floral display and richness of floral resources, availability of alternative resources (represented by simultaneously flowering species), and extrinsic factors, such as climate that affects pollinator activity and demand for resources. It is no surprise then that sensitivity to density is plant and pollinator specific.

(2) Habitat fragmentation

Habitat fragmentation is one of the most pervasive modifications that humans have imposed on the natural landscape. The division of habitats into distinct patches isolates remnant plant populations and may limit gene flow between them as a result of breakdown of plant-pollinator (or plant-seed disperser) interactions (Jennersten, 1988; Aizen & Feinsinger, 1994*b*; Didham *et al.*, 1996; Kearns *et al.*, 1998; Cunningham, 2000*a, b*). Few studies have actually quantified pollination success in habitat fragments, and recorded declines of seed set could instead be explained by the various environmental changes associated with the process and outcome of fragmentation. Nevertheless, experimental studies and field observations have shown that habitat fragmentation causes a decline in pollinator abundance (Jennersten, 1988; Aizen & Feinsinger, 1994*b*; Liow, Sodhi & Elmqvist, 2001; Lennartsson, 2002) and limits pollinator movement among patches (Steffan-Dewenter & Tscharrntke, 1999; Goverde *et al.*, 2002). Plants occupying fragmented habitat patches may therefore receive fewer flower visits (Jennersten, 1988; Lamont, Klinkhamer & Witkowski, 1993; Schulke & Waser, 2001), smaller pollen loads (Cunningham, 2000*a*) or poor pollen quality (Severns, 2003), all of which depress seed set. Limited pollen flow between geographically isolated patches increases inbreeding (Richards, Church & McCauley, 1999; Richards, 2000) resulting in progeny that are less fit as a result (Ågren, 1996; Hendrix & Kyhl, 2000; Lennartsson, 2002; Severns, 2003).

The nature and scale of the surrounding habitat matrix can further influence the likelihood or extent of reproductive decline. In Sweden seed set of the herbaceous grassland perennial *Gentianella campestris*, experimentally reintroduced into grasslands of various sizes, decreased non-linearly with increasing local fragmentation by juniper scrub (Lennartsson, 2002). Thresholds occurred at 45–65 % habitat loss in the largest grassland sites but only 30–45 % loss in smaller grassland sites. Bumblebees responded to habitat discontinuity over a relatively narrow range of habitat loss which itself was determined by the overall size of the grassland community. Furthermore, bumblebee abundance was correlated with *G. campestris* patch size, but large grassland sites tended to have a higher abundance of

pollinators than small sites (Lennartsson, 2002). Bumblebees responded to habitat discontinuity at much smaller scales than might be suggested by their flight capacities and foraging ranges, possibly because patches were fragmented by bushes that could have obstructed pollinator mobility and visual acuity (Lennartsson, 2002).

The implicit assumption so far has been that the intervening matrix between habitat patches or isolated trees is hostile or unfavourable to animal movement across it. More realistically, the effects of habitat fragmentation on mutualists of plant reproductive processes is a function of their vulnerabilities to the new habitat mosaic in addition to the pattern and extent of fragmentation. There are many examples of wide-ranging generalist species that perform as well as, if not better, in fragmented landscapes compared to undisturbed continuous habitats (e.g. Ådren, 1994; Bowne & Bowers, 2004). Habitat fragmentation may cause a decline in the abundance of habitat specialists, but the expected loss of the pollinator or seed disperser functions that they provide may be compensated by increasing abundance of generalists that fulfil similar functions (Aizen & Feinsinger, 1994*b*; Hurlin, 1997; Dick, 2001). More subtle indirect impacts on plant reproduction may result from the changing foraging and dispersal behaviour of mutualistic partners. Most obviously, pollinators or seed dispersers may avoid crossing new unfamiliar habitats, thereby limiting gene flow by pollen or seed. On the other hand the foraging areas of generalists may be little affected, but the consistency of visits to particular plant species may decline, resulting in reduced pollen quality and less frequent seed dispersal (or dispersal to unfavourable areas) for those species. It is further possible that pollinators and seed dispersers may preferentially forage in the novel habitats of the matrix, particularly when a super-abundance of resources is available, for example certain agricultural crops or invasive species. Local site fidelity to resource-rich areas may restrict gene flow of natural native species even further (e.g. Visscher & Seeley, 1982).

Reproductive isolation of plants in patches is therefore mediated by the foraging ranges and behaviour of their pollinators. Gene flow between widely separated fragments may be sustained if pollinators readily move across large distances. Generally, large pollinators have greater capacity to cross gaps between fragments, and pollinators visiting the most isolated fragments tend to have large bodies (Steffan-Dewenter & Tscharrntke, 1999). In Mexican fragmented forest flower visitation by small *Glossophaga* spp. bats was lower than in adjacent undisturbed forest (Quesada *et al.*, 2003; Quesada *et al.*, 2004) probably due to a small home range of 2–4 ha (Fleming, Nunez & Sternberg, 1993), while the larger *Leptonycteris curasoae* with a home range of several square kilometres (Horner, Fleming & Sahley, 1998) occurred equally frequently in both areas. Large bees and hummingbirds are able to traverse several hundred metres (Jennersten, 1988; Schulke & Waser, 2001; Dick *et al.*, 2003) and bats several kilometres (Law & Lean, 1999) of resource-poor land so plants pollinated by these groups may be less susceptible to fragmentation-induced reproductive decline. However, the behaviour of pollinators needs to be considered simultaneously with their capacity for long flights

(Nielsen & Ims, 2000). Bumblebees and honeybees, for example, often groom pollen from their bodies while flying which reduces their effectiveness as long-distance pollinators (Proctor, Yeo & Lack, 1996). Bumblebees can also be highly site-constant moving pollen only a few metres (Osborne & Williams, 2001) and, as described above, may be more or less sensitive to fragmentation depending on the qualitative nature of the fragmenting medium. Thus the scale at which different pollinators view the landscape as fragmented is subject to their mobility (Thomas, 2000) but the repercussions to plants are further mediated by the vagaries of pollinator behaviour.

Not all studies of seed set and pollination in fragmented habitats have been unequivocal in their findings. In a comparative assessment of flower production, seeds per fruit, fruit per inflorescence and fruit predation among variably sized fragments for four species from open dry Mallee woodland in Australia, Cunningham (2000*b*) found only a single variable in one species (fruit per inflorescence in *Acacia brachybotrya*) for which there was evidence of an overall fragment size effect. While it was clear that habitat fragmentation affected several elements of reproductive success among the four plants, the overall impacts on seed production could not be easily linked to habitat fragmentation.

Fragmentation affects plant population genetics by loss of alleles through drift and by inbreeding. Pollinators in fragmented landscapes may exacerbate inbreeding in small patches if they avoid moving between habitat patches (Severns, 2003) or change their foraging behaviour. Thus normally traplining hummingbirds adopt territorial behaviour at isolated *Symphonia globulifera* trees, securing pollination and elevated seed set for the tree albeit at the cost of increased proportion of selfed seeds (Aldrich & Hamrick, 1998). A similar change in foraging behaviour has been observed at patches of *Betonica officinalis* by bumblebees which visited more inflorescences and tended to remain longer in smaller patches (Goverde *et al.*, 2002). However, pollinators that readily move between patches may even disperse pollen further than they had in previously contiguous habitat (Hendrix & Kyhl, 2000; Dick *et al.*, 2003). Such 'overdispersal' of pollen may counter inbreeding, but can also be detrimental if there is significant outbreeding depression. While the distance pollen is moved in a fragmented landscape can exceed that in a continuous habitat, there is generally a decrease in the genetic diversity of progeny owing to fewer pollen donors (Aldrich & Hamrick, 1998; Cascante, *et al.*, 2002; Dick *et al.*, 2003).

Genetic studies have demonstrated that pollen from some tropical trees can be dispersed great distances across fragmented forest landscapes (Chase *et al.*, 1996; Aldrich & Hamrick, 1998). Single apparently isolated trees in the surrounding habitat matrix can provide an important 'stepping stone' function for pollen movement thereby linking subpopulations and they can even dominate population reproduction (Aldrich & Hamrick, 1998). The patterns of pollinator movement between habitat fragments are likely to be contingent on the distribution of appropriate floral resources in the intervening habitat matrix which act to reduce landscape discontinuity from the pollinators' perspectives.

Recent genetic analyses have concluded that wind-pollinated trees may be pollen limited and that pollen movement by wind might be spatially very restricted (Allison, 1990; Sork, 1993; Knapp *et al.*, 2001; Koenig & Ashley, 2003). Increased fragmentation could, therefore, lead to reproductive failure in some wind-pollinated species, but too few studies are available to separate out the effects of population size from fragment isolation (though see Knapp *et al.*, 2001).

(3) Population size

Few studies have separated the effects of habitat fragmentation or plant density from population size, that is the number of individuals in a local population. Most field studies do not distinguish between these elements of plant abundance even to the extent that fragmentation and density are often used interchangeably with population size. It is clearly difficult to separate these effects under natural field conditions. Instead we rely on carefully constructed experimental studies to tease apart the relative importance of population size and population isolation to pollinator behaviour and seed set. The few experimental studies that have manipulated population size while maintaining constant density have not shown significant effects of population size on pollination (Campbell, 1985; van Treuren *et al.*, 1993; Kunin, 1997; but see Hackney & McGraw, 2001) while studies of natural populations have produced mixed results with increases (Sowig, 1989; Aizen & Feinsinger, 1994*a*), decreases (Sih & Baltus, 1987; Lamont *et al.*, 1993; Aizen & Feinsinger, 1994*a*; Ågren, 1996; Ghazoul & McLeish, 2001; Jacquemyn, Brys & Hermy, 2002; Paschke, Abs & Schmid, 2002; Forsyth, 2003; Severns, 2003; Aguilar & Galetto, 2004) and no obvious effects (Campbell & Motten, 1985; Sowig, 1989; Aizen & Feinsinger, 1994*a*; Costin, Morgan & Young, 2001; Bosch *et al.*, 2002; Murren, 2002; Somanathan, Borges & Chakravarthy, 2004) of pollination or reproductive output in small populations. Bearing in mind the tendency for negative or non-significant results to be underreported in the scientific literature, the balance of these field studies coupled with results from experimental studies suggests that the effect of population size on pollination is markedly less important than that of population density or fragmentation. Despite this equivocal conclusion several field studies, described below, representing a range of life forms and pollinator types show that small populations are at a reproductive disadvantage, so further study is warranted.

A relationship between population size and seed set through pollination effectiveness has been observed in self-incompatible animal- (Sih & Baltus, 1987; Ågren, 1996; Ghazoul & McLeish, 2001; Jacquemyn *et al.*, 2002; Paschke *et al.*, 2002; Forsyth, 2003; Severns, 2003; Aguilar & Galetto, 2004) and wind-pollinated plants (Nilsson & Wastljung, 1987; Knapp *et al.*, 2001). Depressed pollination may also be a feature of small populations of self-compatible plants that are nevertheless able to retain high seed set through selfing (Bosch *et al.*, 2002). It has been argued that small plant populations are generally less attractive or less apparent to pollinators than are large populations (Sih &

Baltus, 1987; Jennersten & Nilsson, 1993; Ågren, 1996) leading to a decline in pollinator visits and poor pollen quality (Silander, 1978). Fruit set of *Banksia goodii*, for example, declined precipitously to zero as population size decreased (Lamont *et al.*, 1993) as its bird pollinators avoided populations below a certain size. In the Haleakala silversword *Argyroxiphium sandwicense* seed set was correlated with the number of flowering plants in a population which varied from 167 to 2687 plants during a five-year study (Forsyth, 2003). The plants were pollen limited when flowering was asynchronous, but not during periods of synchronous flowering when seed set was correspondingly much higher (Forsyth, 2003). However it remains unclear whether this outcome was a result of population size or density (or a combination of the two). Lower pollination intensity of the herkogamous *Primula elatior* in small populations (4 to approximately 50 plants) contributed to declining fecundity which may have been exacerbated by skewed pin-thrum ratios in small populations (Jacquemyn *et al.*, 2002, Kery, Matthies & Schmid, 2003). Seed set of *Rutidosia leptorhynghoides*, an endangered daisy occurring in variously sized population patches in grasslands of south-eastern Australia, was also depressed at small population sizes (<30 plants), but this simple pattern can, in some years, be confounded by other environmental stresses such as drought (Morgan, 1999). Seed set, but not pollination, of *Anacardium excelsum* in Costa Rica was positively correlated with population size up to approximately 30 trees with little change thereafter (Ghazoul & McLeish, 2001), which was explained by low pollen quality in small populations due to inbreeding. On the other hand, Costin *et al.*, (2001) reported no effects on seed production of the perennial herb *Leucochrysum albicans* across a population size range of 74 to over 50 000 plants.

Among wind-pollinated species pollination success is largely a function of population pollen production which is correlated with the abundance and density of individuals. Indeed, depressed seed set (Nilsson & Wastljung, 1987; Smith *et al.*, 1988; Knapp *et al.*, 2001) or reduced outcrossing (Perry & Knowles, 1990) has been noted for several wind-pollinated trees occurring at low density or in small populations. As many wind-pollinated species are dioecious a thinning of the population that skews sex ratios in favour of female plants may reduce seed production by insufficient pollen production (Shibata, Tanaka & Nakashizuka, 1998).

Population or patch size and local density can interact such that isolated plants in small populations have most risk of being pollen limited (Groom, 1998). Thus *Clarkia concinna* seed set as a function of density was pronounced in the smallest populations, but once population size exceeded 50 individuals no clear relation between seed set or pollen receipt and isolation could be detected (Groom, 2001). The widely reported correlation of population size with density may therefore lead to pollination failure through both density and abundance mechanisms. Conversely, among populations of *Primula elatior* population size and plant density were correlated but their impacts on seed production were expressed differently (Jacquemyn *et al.*, 2002): small populations had reduced seed set, but fruit abortion was higher at high plant densities as a result of inbreeding among near neighbours.

These field studies highlight several possible reasons for reported positive associations of seed set or pollination success with population size. Small populations of outcrossed animal-pollinated plants may be less attractive to pollinators (Jennersten & Nilsson, 1993; Ågren, 1996) and have fewer individuals with which to breed thus reducing the availability of compatible pollen (Young, Boyle & Brown, 1996; Ghazoul & McLeish, 2001). Pollen quality may be eroded further if loss of purity accompanies population decline, and small populations are also more likely to be inbred (Ellstrand & Elam, 1993; Ghazoul & McLeish, 2001). Yet all these studies recorded effects on fecundity only when populations were very low – usually less than 50 plants – and when no clear population size effects were reported the smallest populations always exceeded 50 individuals (see for example, Cunningham, 2000b; Costin *et al.*, 2001). Populations as small as these become vulnerable to a host of other factors that could cause extinction. Thus small populations of *Clarkia concinna* became extinct not due to reproductive failure *per se* but rather to chance environmental events (Groom, 1998). Nevertheless, Allee effects at very low population sizes may add to the difficulties for recovery of rare or highly fragmented plant populations.

(4) Population purity

Declining purity can lead to competition for pollinators among simultaneously flowering plants (Kunin, 1997; Ghazoul, 2002a, 2004) resulting in reduced visitation to any single species and low floral constancy (the propensity to visit the same type of flower as last visited). Pollinators appear generalist in their selection of flowers where no single flowering dominates (Kunin, 1993) but respond in a frequency-dependent manner where one or a few plant species dominate the floral community (Epperson & Clegg, 1987; Smithson & Macnair, 1996). Such outcomes can become particularly severe if a decline in the abundance of a previously common or dominant species is coupled with the simultaneous increase in one or several other species that have the potential to compete for pollinators (Ghazoul, 2004).

The role of purity is more complicated for non-rewarding plants that gain pollination services through deception. Pollinators learn to avoid non-rewarding plants that are encountered frequently, that is under conditions of high local purity (Ferdy *et al.*, 1998), while at low densities they face the same constraints with regard to pollinator attraction and pollen quality as other plants. Thus pollination of non-rewarding deceptive plants is expected to be optimal at intermediate levels of purity (Alexandersson & Ågren, 1996). Furthermore, the spatial scale over which deceptive plants co-occur with nectar-producing 'magnet' plants is important in determining the pollination success of the deceptive species (Johnson *et al.*, 2003). Pollination of the deceptive bumblebee-pollinated orchid *Anacamptis morio* was more successful where it occurred with nectar-producing plants, but this result was scale dependent being stronger at larger scales of 100 m² to 1 ha (Johnson *et al.*, 2003).

Of wider relevance is the spread of exotic invasive plants that compete with indigenous species for pollinators and

reduce their purity. Regeneration by seed of alien plants in a novel environment is usually dependent upon the procurement of indigenous pollinators that may lead to competition for pollinators between natives and aliens. Increasing demand for pollinator attention may even create conditions of pollinator limitation where previously there were none. Many highly successful, that is invasive, alien plants are profligate in their production of flowers and floral resources (Brown & Mitchell, 2001; Ghazoul, 2002*b*). The number and size of flowers, nectar content and pollen production of invasives often greatly exceeds that of morphologically or taxonomically similar natives. Such plants are likely to represent a more attractive pollinator foraging venue at the expense of attention to native species. Successful competition for pollinators by invasive species has now been noted in a number of experimental and natural conditions (Chittka & Schurkens, 2001; Brown, Mitchell & Graham, 2002; Ghazoul, 2002*a*, 2004). Purple loosestrife *Lythrum salicaria*, an invasive perennial shrub in North America, reduced both pollinator visitation and seed set of its native congeneric winged loosestrife *L. alatum* in experimental arrays (Brown & Mitchell, 2001). Compared to its congener, *L. salicaria* produces approximately four times as many flowers and twice as much pollen per flower, representing a more attractive display and greater rewards than the less showy native plant. In addition to securing the bulk of pollinator visits, abundant pollen production by *L. salicaria* compromised the quality of pollen received by *L. alatum*. Interspecific pollen transfer reduced seed set of *L. alatum* possibly by stigmatic clogging, or by interference with pollen germination or pollen tube growth (Brown & Mitchell, 2001).

Competition for pollinators may also occur between widely different and unrelated species. Butterfly pollinators of *Dipterocarpus obtusifolius*, a dipterocarp tree in Thailand, were preferentially attracted to the invasive shrub *Chromolaena odorata* resulting in reduced visitation and pollen quality at *D. obtusifolius* flowers (Ghazoul, 2002*a*, 2004). The butterfly pollinators responded to the invasive plant by changing the location of their foraging activity from *D. obtusifolius* canopies to the forest understory where *C. odorata* presented its flowers. In this case there was ultimately no impact on seed set of *D. obtusifolius* due to a diversity of pollinators, including moths and birds, and some compensatory pollination by other butterfly species. A similar story has been noted in Europe where the highly successful invasive Himalayan balsam *Impatiens glandulifera* draws pollinators away from native plants by offering much richer floral rewards (Chittka & Schurkens, 2001). At least one native plant suffered reduced seed set where *I. glandulifera* occurred.

In addition to being effective competitors for pollinators, invasives also tend to have extended flowering periods that may encompass those of several natives. *Lantana camara*, a central American plant has become widespread in tropical Asian and African regions, produces flowers and seed almost year round. Another American invasive *Mimosa pigra* has a five-month flowering period. Thus a single invasive may affect the purity of several sequentially flowering natives.

The impact of invasives or dominant species on the native floral community might not always be negative, as they may facilitate the attraction of pollinators to patches that include

rarer plants which would otherwise not receive pollinator visits (Rathcke, 1983; Memmott & Waser, 2002). Floral resources offered by dominant species or invasives may also benefit native plants flowering much later by maintaining pollinator populations at high levels (Waser & Real, 1979; Memmott & Waser, 2002).

It is as yet uncertain to what extent the rapid spread of alien species into novel environments will alter native plant-pollinator interactions by decreasing the purity of natives and by direct competition. The conditions under which this might occur appear sufficiently restrictive – overlapping flowering periods, shared generalist pollinators, pollinator limitation, seed-limited recruitment – that perhaps only a few native species are likely to be adversely affected in this way. On the other hand, immense and prolonged floral productivity of many invasives coupled with predominantly generalist pollination systems of most plants (Waser *et al.*, 1996) could very well satisfy these conditions in many cases, leading to the widespread procurement of native pollinator services at the expense of natives.

(5) Drawing conclusions from current studies

The recent accumulation of studies on plant reproductive ecology in changing landscapes, listed in Table 1, permits some analysis of the frequency with which Allee effects are observed and assessment of vulnerabilities of plants according to their breeding system and life form. The summary of the responses of plant species to density, patch size, purity and population size, presented in Table 2, shows that in almost all categories there is a strong tendency towards demonstrated Allee effects. In the most equivocal case where the number of studies is low (pollination responses to plant purity) still more than half the studies show significant responses. Even allowing for biases against the reporting of no effects, the balance of results appears sufficiently strong to suggest that Allee effects among plants are not uncommon. There are no obvious differences among the spatial attributes in terms of the likelihood of their impacts on pollination ($X^2 = 1.88$, d.f. = 3) or reproductive output ($X^2 = 4.26$, d.f. = 3). Local plant density, population size and purity show clear effects on reproductive output, although the overall picture for patch size is much more equivocal. This may simply reflect a greater number of studies on patch size coupled with an increased tendency for negative (non-significant) results for all spatial variables to be published in more recent years (Fig. 3).

Further analysis of Table 1 shows, contrary to expectation, that breeding system has no significant influence on likelihood of Allee effects on fruit or seed production ($X^2 = 1.16$, d.f. = 1; see Table 3). This result reflects that of Aizen *et al.* (2002) who considered pollinator visitation rather than reproductive output. Thus self-compatible plants appear just as vulnerable to Allee effects as self-incompatible plants, although it is worth repeating the potential bias, also mentioned by Aizen *et al.* (2002), arising from the tendency for researchers to select plants that depend on pollinators for seed set regardless of breeding system.

Life form appears to have no effect on susceptibility to Allee effects (Table 4) with regards to pollination ($X^2 = 1.23$,

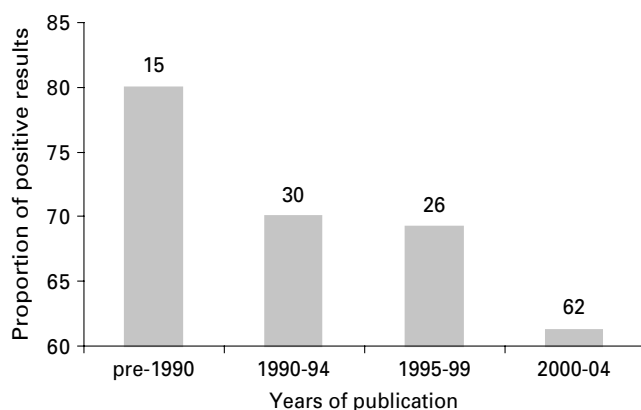


Fig. 3. The ratio of significant to non-significant Allee responses of plant species as reported in the literature since 1972. The graph shows the proportion of significant responses which declines in more recent years suggesting that any existing bias against the reporting of negative results is declining. Allee effects may therefore affect fewer species overall than has been previously indicated by perusal of studies prior to 2000. Total number of species within each category is given above the bars. Data derived from Table 1.

d.f. = 2) or reproductive output ($\chi^2 = 2.33$, d.f. = 2). All things being equal, Allee effects are more likely to affect population persistence of short-lived herbs by affecting lifetime fitness, whereas trees and shrubs have more opportunity to compensate for periods of low seed set by virtue of a long life span. Thus herb species which have most to lose are expected to have characteristics (such as selfing or clonal reproduction) that decrease their sensitivity and vulnerability to Allee effects. Based on the current set of studies there is no evidence to suggest that herbaceous plants are any less susceptible to short-term Allee effects than any woody perennials.

In conclusion, there is abundant evidence demonstrating that Allee effects among plants are widespread and commonly observed among species from a wide variety of taxa, life forms and breeding systems.

V. THE IMPORTANCE OF POLLINATOR BEHAVIOUR, ABUNDANCE AND DIVERSITY

(1) Pollinator behaviour and type

As agents of pollen transfer, the foraging behaviour of pollinators is crucially important to pollination success and seed set in pollen-limited plants. Elements of pollinator behaviour that are relevant to plant reproduction and spatial isolation are search behaviour, foraging range and diet breadth. Pollinator responses to changes in resource abundance and distribution depend on a combination of these elements, and may entail a switch to alternative resources or an expansion of foraging range to encompass additional individuals. The implications for plant populations of such responses are dramatically different, yet despite this almost nothing is known about the general foraging patterns of

Table 4. Distribution of studies describing effects of plant spacing on pollination and reproductive output among herbs, shrubs and trees. Measures of 'pollination' include pollinator visitation, pollen deposition on style or abundance of pollen tubes. Reproductive output included seed and fruit production. Studies that recorded several variables within each category are scored only once, and scored as a positive result if at least one variable was subject to an Allee effect. Data are derived from Table 1.

	Pollination	Reproductive output
Trees		
Allee effect	14 (67)	15 (62)
No effect	7 (33)	9 (38)
Shrubs		
Allee effect	7 (54)	9 (50)
No effect	6 (46)	9 (50)
Herbs		
Allee effect	29 (71)	41 (69)
No effect	12 (29)	18 (31)
Total	75	101

most pollinators beyond very local and short-term foraging decisions.

At local scales pollinator foraging behaviour is strongly linked to the availability of floral resources. Where floral displays are large and resources locally rich most pollinator flights are made among neighbouring flowers within a plant (Barrett & Harder, 1996; Ohashi & Yahara, 2001; Barrett, 2003) increasing the likelihood of self-pollination, but also increasing the number of flowers visited both by virtue of individual pollinators probing more flowers per plant and by attracting more pollinators in the first place. At larger spatial scales, of tens to hundreds of metres, floral display size is expected to become increasingly important as plant density decreases because of the need to attract pollinators from further away (Willmer *et al.*, 1994) and because the increasing cost to pollinators of interplant movement favours visits to more rewarding plants (Harder & Barrett, 1995; Kunin, 1997). Thus there is a trade-off in floral display size between on the one hand the need to attract many pollinators (pollinator quantity), and on the other, the risks of inbreeding (pollination quality). The relevance of the trade-off (and importance of display size) to plant reproduction is mediated by plant density (Fig. 4). Modelling pollinator responses to various floral display sizes under differing plant densities suggests that the benefits of attracting pollinators by larger floral displays do not counteract the costs of increased selfing even with large pollinator availability and pollen carryover (Ohashi & Yahara, 2001), although these results are not always supported by empirical study (Mustajärvi *et al.*, 2001). Furthermore, even a small rise in the cost of interplant movement is predicted to increase the costs of geitonogamy dramatically on large displays (Ohashi & Yahara, 1999).

The constancy with which pollinators visit plant species is relevant to the quality of pollen received at flowers. Generalist pollinators are more likely to carry a diverse

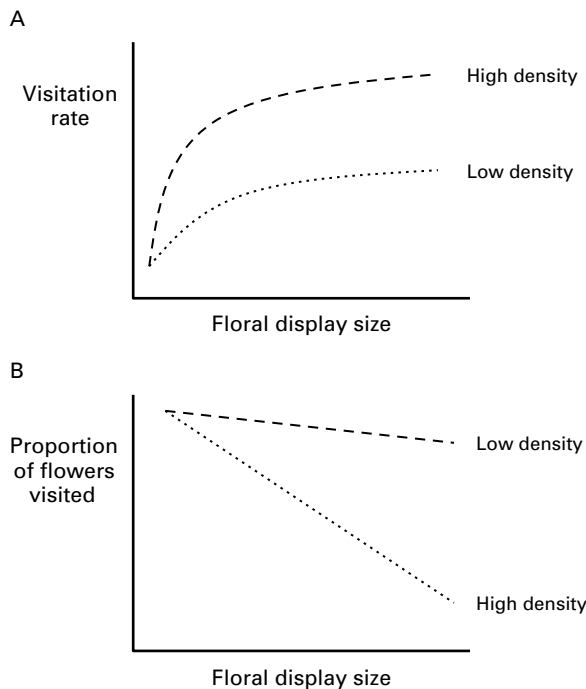


Fig. 4. The relationship between floral display size and (A) pollinator visitation rate, and (B) proportion of flowers visited per plant, at high and low plant densities. Pollinator visitation and the number, rather than proportion, of flowers visited per plant increases as floral display size increases, but the strength of this relationship is dependent on local plant density. In high-density situations visitation increases more rapidly and reaches a higher asymptote, but a smaller proportion of flowers are visited. Figure derived from models of Ohashi & Yahara (2001) and other empirical studies.

array of pollen types only a small proportion of which is compatible to each visited flower. Rare plants are particularly susceptible to transfer of inter-specific pollen as generalist pollinators forage in a frequency-dependent manner showing greater constancy to common species or floral morphs (Epperson & Clegg, 1987; Smithson & Macnair, 1997a; Smithson & Macnair, 1997b) with disproportionate costs for rare species. Common flowers are probably more apparent to pollinators but, additionally, pollinators may improve foraging efficiency by specialising on the most common flower types. Some studies have been unable to detect frequency-dependent foraging (Waser, 1982) and Smithson & Macnair (1997a, b) argue that positive frequency-dependent selection is only likely to be important to reproductive success if pollinators are rare.

The pattern and capacity of pollinator movement contributes greatly to the efficiency of animals as pollinators. Animals and insects that are capable of crossing large distances in flight have the potential to promote outcrossing between plants that are widely separated in space. Tropical hummingbirds and euglossine bees, for example, commonly visit plants sequentially over a wide geographic area (traplining) (Janzen, 1971; Linhart & Feinsinger, 1980). Bats

are known to transfer pollen between trees over distances of several kilometres (Law & Lean, 1999) and between forest patches in a fragmented landscape. Nevertheless, a capacity for long-distance flight does not equate to extensive pollen transfer. Some large euglossine bees show local site fidelity despite being capable of covering large areas in a 'traplining' fashion (Ackerman *et al.*, 1982). Forest honeybees may show fidelity on a daily basis to very small patches (a few tens of metres wide) even though the location of the patch may be several kilometres from the nest (Visser & Seeley, 1982). Other pollinators (largely bees) are territorial and tend to move pollen only among one or a few adjacent plants (Feinsinger *et al.*, 1986; Willmer *et al.*, 1994). Bumblebee behaviour appears conditional on the distribution, size and density of rewarding patches: bumblebees in fragmented landscapes visit more flowers more intensively in small fragments than in large fragments or continuous habitat (Rasmussen & Brodsgaard, 1992; Cresswell, 1997, 2000; Goverde *et al.*, 2002), while directionality of bumblebee flight decreases with increasing plant density (Cresswell, 1997), and edge plants provoke changes in direction or reversals (Rasmussen & Brodsgaard, 1992). Some pollinators (honeybees and butterflies) readily move between patches while others (beeflies) typically return to a profitable patch if they fail to encounter another within a few metres (Groom, 1998). Bumblebees foraging on *Senecio* species tended to visit near neighbours and visit many heads per plant, whereas butterflies visiting the same plants moved much greater distances and were more effective agents of gene flow (Schmitt, 1980). Even congeners can differ markedly in their foraging behaviour – of two species of *Trigona* bee in Costa Rica one forages in large groups on dense flowering patches while the other forages individually or in small groups visiting widely spaced plants (Johnson & Hubbell, 1975).

Interactions among pollinators at plants can affect the dynamics of pollination. Increasing pollinator activity during periods of high flowering density can lead to an increase in aggressive interactions among territorial bees (Frankie *et al.*, 1976) and birds (Smith-Ramirez & Armesto, 2003). In consequence the number of inter-tree movements by bees, and presumably outcrossing, is increased. Predators of pollinators may also be attracted to high densities of mass flowering trees which promotes movement of pollinators to other trees to avoid predation (Gentry, 1978).

Pollination by beetles, flies, butterflies and moths is particularly common in tropical regions. Beetles can travel relatively long distances between successive flower visits (Sakai *et al.*, 1999) and can be important in contributing to cross pollination. Flies can carry substantial pollen loads (Kearns, 1992) but move relatively short distances (up to a few metres) between plants (Olesen & Warncke, 1989; Widen & Widen, 1990). Many moths also have large pollen loads (Willmott & Burquez, 1996) and may cover considerable distances (up to 400 m) between successively visited plants (Linhart & Mendenhall, 1977). Butterflies disperse pollen to similar distances as moths but carry comparatively small amounts of pollen (Murawski & Gilbert, 1986). High floral constancy, and hence pollen quality, has also been reported for beetles, flies and lepidopterans.

The spatial scale over which pollinators respond to variation in plant display size depends on plant spatial distributions, pollinator identity, pollinators' energetic requirements, visual acuity and number of competitors, and the availability of alternative resources. Understanding how these factors interact to contribute collectively to pollinator foraging decisions at anything larger than very local scales is currently not within our grasp.

(2) Pollinator population size and local abundance

Concern about regional declines in pollinator abundance following changes in land use has been expressed in recent years (Allen-Wardell *et al.*, 1998), although the actual extinction of pollinators has very rarely been recorded (though see Washitani, 1996) except in island systems (Cox & Elmqvist, 2000). Insect pollinators may be more sensitive to particular habitat characteristics at small spatial scales such as vegetation cover, dead wood, or per cent grassland, than to landscape features such as fragment size or plant population distributions (Gess & Gess, 1993; Donaldson *et al.*, 2002). At local scales declining abundance or density of floral resources has been cited as a cause of pollinator deficits acting through reduced pollinator population sizes (Sih & Baltus, 1987; Jennersten, 1988; Aizen & Feinsinger, 1994*a, b*; Cunningham, 2000*a*; Paton, 2000; Liow *et al.*, 2001) which, in turn, depresses the reproductive output of remaining plants (e.g. Cunningham, 2000*a*; Lennartsson, 2002) drawing both pollinator and plant into an increasingly steep extinction vortex. Other studies have shown that while pollinator abundance may decline with increasing distance from relatively contiguous habitat, the richness and composition of pollinator communities is, for the most part, unaffected by habitat fragmentation (Donaldson *et al.*, 2002). High densities of flowering plants, sufficient to support high diversity and abundance of pollinators, can be found in even very small (<1 ha) fragments (Webb, 1989; Kemper, Cowling & Richardson, 1999). This generalisation, however, hides certain species-specific responses. Thus the abundance of *Rediviva* spp. bees that are specialist pollinators of the oil-producing orchid *Pterogydium catholicum* may be so low in small fragments that seed set is reduced to zero (Donaldson *et al.*, 2002). Pollinators may also respond in a species-specific manner to different scales of landscape change (Steffan-Dewenter *et al.*, 2002). For example, the abundance of solitary bees was strongly associated with percentage cover of semi-natural habitat at scales up to approximately 2 km², whereas honeybees showed no response at such scales but rather increased with declining semi-natural habitat at the largest scales tested of 28 km² (Steffan-Dewenter *et al.*, 2002).

When several species of plants that share pollinators occur together at low density they may have a facilitatory effect in attracting and supporting pollinator populations. The risk remains that pollinators in such conditions will carry the pollen of several species and hence the quality of transferred pollen is likely to be low. As has already been described, pollinator behaviour can change at different densities, with some species (e.g. bumblebees and hummingbirds) becoming less discriminate at low densities.

Where pollinator populations are low rare plants may initially benefit by the facilitatory attractiveness of other locally flowering rare species, but if one of these species becomes relatively common any early facilitation may be lost as pollinators begin to specialise on the more abundant species (Kunin, 1997) resulting in both reduced visitation of rare plants and increased likelihood of transfer of non-specific pollen. On the other hand, as flower density increases pollinators may indeed become more abundant, but also more sedentary or territorial (Willmer *et al.*, 1994; Osborne & Williams, 2001) leading to reduced gene flow.

In highly specialised fig–fig wasp pollination systems each mutualistic partner is obligately dependent on the other such that the quality of the reward received, be it pollen for fig wasps or pollination for figs, is generally considered to be high and reliable. This assumes pollinators are sufficiently abundant that enough are able to locate their host plants. A single *Ficus* spp. tree typically produces syconia in brief and highly synchronised events, but considerable asynchrony among trees results in the near-continuous availability of fig syconia through the year. As fig wasps are short-lived and have no diapause, population persistence is dependent on there always being at least one tree with syconia containing developing wasps. A decline in the abundance of *Ficus* spp. trees (through forest degradation, tree destruction, habitat fragmentation *etc.*) may result in one or more interruptions in the continuous availability of syconia which, if such gaps exceed fig wasp life spans, would cause a crash in pollinator populations. Even a syconium-free period of a few days may be sufficient to cause fig wasp population collapse and consequently reproductive failure of figs. A marked decline in pollinator activity following temporary non-availability of syconia has been observed in some Mexican populations of *F. insipida* (Smith & Bronstein, 1996). Nevertheless, this seemingly precarious reproductive system appears very resistant to change and no cases of long-term reproductive failure have been described, although individual trees commonly abort all syconia due to lack of pollination (James Cook, personal communication). One possible exception is when severe drought in 1997–98, linked to an El Niño event, caused substantial discontinuity in the production of inflorescences in dioecious figs in northern Borneo leading to the local extinction of fig-wasp pollinators (Harrison, 2003). Pollinators remained absent for six months after the drought, with clear implications for fig pollination, at least in the short term. Nevertheless, the apparent widespread resistance of fig reproductive systems to environmental change may be due to enormous fig wasp dispersal, which has been shown to be effective over tens of kilometres in tropical forests (Chase *et al.*, 1996; Nason *et al.*, 1998) and over 80 km across arid landscapes (Ahmed, 2003). Relaxation of within-tree synchrony of the fig sexual phase would also lessen the likelihood of occasional occurrence of population-wide non-flowering phases. Within *Ficus* there is indeed considerable variability among species in within-tree synchronisation of syconia production (Smith & Bronstein, 1996), but whether this is correlated to plant rarity, seasonality, and/or pollinator dispersal abilities remains to be seen. One phenological study does show that within-tree crop synchrony is least among populations

occupying drier sites where fig populations were smaller and more isolated (Smith & Bronstein, 1996).

Owing to naturally large population fluctuations of insects, even in relatively stable environments (Roubik, 2001), it is difficult to ascribe the abundance observed in one year to a long-term persistent trend. Concern over the functional decline of pollinators, in the tropics at least, may therefore have been overstated. Indeed, bee communities may be more resistant to habitat fragmentation than previously thought (Cane, 2001) and a more likely outcome of fragmentation may be the rather more subtle changes in pollinator foraging patterns described above.

(3) Pollinator diversity

The diversity of a pollinator community can, in some cases, be a better predictor of fruit set than pollinator abundance (Donaldson *et al.*, 2002; Kremen, Williams & Thorp, 2002; Klein, Steffan-Dewenter & Tscharntke, 2003). A speciose pollinator community interacts with plants across a wide range of spatial and temporal floral resource distributions, while random sampling effect ensures that efficient pollinators are more likely to be represented. The pollination service provided by a diverse pollinator community is also less susceptible to annual fluctuations in pollinator populations (Kremen *et al.*, 2002). The richness of pollinators supported by a landscape is affected by the distribution and composition of habitats within it (Gess & Gess, 1993; Donaldson *et al.*, 2002; Steffan-Dewenter *et al.*, 2002). Distance from forest fragments, for example, is known to affect the abundance and diversity of tropical social bees that depend on fragments for nesting sites (Liow *et al.*, 2001; Klein *et al.*, 2003), while the type of vegetation, percentage grass cover and rockiness of surface may determine the local abundances of pollinating monkey beetles (Donaldson *et al.*, 2002), and it has already been mentioned above that a high local flowering plant richness may support a rich pollinator community in even the smallest of fragments (Webb, 1989; Kemper *et al.*, 1999). Thus a complex and apparently mutually dependent interaction exists at the community level between plants and pollinators: high plant richness favours high pollinator diversity that in turn maintains high plant richness.

VI. PLANT SPATIAL DISTRIBUTION AND SEED DISPERSAL

Dispersal of pollen is only one mechanism by which gene flow is achieved by plants, the other being seed movement. Seed-mediated gene flow accounts for two-thirds of the total genetic neighbourhood size (seed are diploid and pollen haploid) and, where animals are the agents of dispersal, is equally likely to be affected by habitat fragmentation and degradation as pollen flow. The strongly leptokurtic seed shadows of many trees can give rise to potentially acute genetic differentiation among adjacent populations (Hamilton, 1999) that is usually overcome by relatively rare seed-dispersal events among populations. In

fragmented landscapes such rare dispersal events may become increasingly infrequent or impossible owing to changes in the abundance or behaviour of animal seed dispersers, and seed recruitment to isolated patches may dwindle to a point where population continuity ceases to be viable. Thus knowing how seed dispersal processes function in post-disturbance landscapes is an important element in anticipating subsequent changes in species composition (Restrepo, Gomez & Heredia, 1999; Da Silva & Tabarelli, 2000; Graham, Martinez-Leyva & Cruz-Paredes, 2002; Githiru *et al.*, 2002).

Habitat fragmentation is known to affect the abundance and behaviour of birds and mammals that are the primary seed dispersers of most tropical seed-bearing plants (Graham *et al.*, 2002; Luck & Daily, 2003). In Brazilian forest fragments, for example, significantly lower frugivore activity was recorded in smaller fragments despite increased frugivory along forest edges (Galetti, Alves-Costa & Cazetta, 2003). Such responses to fragmentation can affect seed dispersal and recruitment (Graham *et al.*, 2002; Guariguata, Arias-Le Claire & Jones, 2002). Dispersal of *Dipteryx panamensis* seed by rodents was numerically greater in continuous than fragmented forests in Costa Rica, although the reverse was true for another canopy tree *Carapa guianensis* indicating that fragmentation effects on seed fate may be species-specific and a function of the dispersal agents involved (Guariguata *et al.*, 2002). Dispersal of figs by large mammals such as howler monkeys and other primates also appears to be more efficient in a large forest fragment (>600 ha) than in a smaller fragment (40 ha) (Serio-Silva & Rico-Gray, 2002). In Tanzania, recruitment of 31 animal-dispersed trees was three times higher in large fragments (exceeding 30 ha in size) than small fragments, whereas recruitment of eight wind- or gravity-dispersed trees showed no difference, the result being linked to the declining abundance of frugivores in small forest fragments (Cordeiro & Howe, 2001).

Avian frugivore populations are also impacted directly by habitat fragmentation (Estrada *et al.*, 1993; Santos & Telleria, 1994; Estrada, Coates-Estrada & Meritt, 1997; Santos *et al.*, 1999; Graham & Blake, 2001; Cordeiro & Howe, 2003) and associated disturbances such as poaching (Wright & Duber, 2001; Guariguata *et al.*, 2002) leading to reduced dispersal of plant seeds. For example, dispersal of juniper seed declined dramatically in fragmented forests owing to a local decline in thrush populations that form the main seed dispersers (Santos *et al.*, 1999). The effects of disturbance on seed dispersal are often more complex due to responses in the foraging behaviour of frugivorous birds which may be influenced by fruit crop size (Alcantara *et al.*, 1997; Alcantara *et al.*, 2000), the type of habitat in which the fruit-bearing plant is located (Alcantara *et al.*, 1997; Alcantara *et al.*, 2000), and habitat distribution (Graham *et al.*, 2002). Low overall fruit dispersal from wild olive trees *Olea europaea* due to the scarcity of frugivorous birds in disturbed areas masked high inter-individual variation in fruit removal success which was related to heterogeneity in plant traits including fruit size, crop size and ripening phenology (Alcantara *et al.*, 1997). Competition for scarce frugivores in disturbed habitats can therefore result in highly skewed individual contributions to plant recruitment that influences

the genetic structure of future cohorts. Avian frugivores have also been noted to avoid open areas (Alcantara *et al.*, 1997) although such responses may be species-specific with some large and socially dominant frugivores being common visitors to trees isolated in high-intensity sites (Luck & Daily, 2003).

Large-fruited plants generally depend on few species of large-bodied birds and animals for dispersal and their susceptibility to fragmentation is further exacerbated by the synergistic interaction with hunting in fragmented forests which targets such large birds and mammals (Peres, 2000; Wright & Duber, 2001; Guariguata *et al.*, 2002). Wind-dispersed plants on the other hand are likely to be relatively immune from such disturbances. Consequently, shifts in the relative abundance of plants with different seed-dispersal strategies and fruit sizes may be expected in increasingly disturbed tropical landscapes, with small-seeded or wind-dispersed trees being favoured over animal-dispersed trees with large fruits (Tabarelli & Peres, 2002).

Secondary dispersal of seeds by rodents and arthropods can be essential in removing seeds from predation risk and ensuring that they are dispersed into favourable germination microsites (Andresen, 1999, 2001). Habitat fragmentation may diminish populations of dung beetles (Andresen, 2003; Chapman *et al.*, 2003) and ants (Carvalho & Vasconcelos, 1999) which are important agents of secondary seed dispersal, or allow invasion by alien species that do not perform such functions as efficiently as natives (Ness, 2004).

VII. THRESHOLDS

A disproportionate increase in extinction likelihood with declining population size characterises Allee effects, and theoretical studies have identified density or population size thresholds below which extinction is almost inevitable (Kunin & Iwasa, 1996; Veit & Lewis, 1996). It has been more difficult to verify these theoretical results with real population data, although extinction thresholds have been suggested in some studies (Lamont *et al.*, 1993; Groom, 1998). Seed set of *Clarkia concinna*, for example, dropped to zero when isolation distance exceeded 26–104 m depending on patch size (Groom, 1998), and small remnant populations of *Banksia goodii* had complete reproductive failure below a certain threshold patch size (Lamont *et al.*, 1993). Pollinator visitation to the endemic Hawaiian dogwood *Nesohedyotis arborea*, pollinated by syrphid flies, declined precipitously at isolation distances greater than 50 m, with fruit set of over 90% declining to less than 40% at trees isolated by more than 100 m (Percy & Cronk, 1997).

Nevertheless, the existence of thresholds remains uncertain for most species, but where they occur they will probably be mediated by the type of pollinator involved. Thus density thresholds below which there is a precipitous decline in pollination success are likely to be much lower for plants pollinated by agents that move very short distances. Unfortunately very little is known about pollinator movement and behaviour under differing circumstances, and most studies include only a superficial treatment of pollinator foraging,

relying instead on simple assumptions about what the animals do. Foraging models give some insight as to how pollinator behaviour affects thresholds of pollination failure. Such models predict that constancy to a particular floral type will break down at low flower density leading to a sudden acceleration of pollination failure (Kunin & Iwasa, 1996). However, interactions among plants and flower visitors are complex and form highly connected webs (Memmott, 1999) and although plants are often visited by specialised insects they often attract more generalised flower visitors too. Recent work by Cotton, 1998 has shown that contrary to previously accepted truisms hermit hummingbirds are as generalised as other hummingbirds, and in tropical lowland forest many pollinators are both generalised and opportunistic in their flower-visiting behaviours (Momose *et al.*, 1998). Additionally, pollinator visitation may not be the best indicator of seed set, as discovered for *Heterotheca subaxillaris* (Asteraceae) in Texas, whose most effective pollinator in terms of seeds set was the least abundant flower visitor (Olsen, 1997).

VIII. IMPLICATIONS FOR CONSERVATION AND EXTINCTION

The immediate and short-term benefit of investing in the conservation of small populations may be questionable if there are problems with maintaining functional reproductive processes in these systems. However, as Kunin (1997) and Roll *et al.* (1997) point out, population density may be more important to reproductive viability than simply the total number of individuals which appears a poor predictor of reproductive success for all except the very smallest populations. Seed set of small but aggregated or high-density populations may therefore continue to be as plentiful as that of larger populations. Conservation programmes that aim to rescue declining populations often have to trade-off the number of populations against their size. While there may be other good reasons to avoid investing in the very smallest populations, a strategy that targets several small but high-density populations may offer the best return for investment in the short term.

Population purity is becoming an increasingly important issue as exotic plants invade indigenous plant populations. Many plant invasives are successful owing, in part, to profigate production of flowers over a prolonged flowering season. Even where natives are not directly impacted by exotic species, the purity of their floral displays is likely to be affected as exotics begin to compete for native pollinators. Native plants may also have to compete with exotic invasives for seed dispersers. It is not yet clear to what extent such competition for mutualistic partners has impacted native plant populations rather than just facilitated the spread of invasives, but it seems likely that plant-pollinator (and possibly also seed disperser) interaction webs across large areas of the tropics will be irreversibly adjusted in response to the spread of profigate-flowering plants such as *Chromolaena odorata*, *Lantana camara* and *Mimosa pigra*.

Are Allee effects alone enough to cause precipitous population declines leading to extinction? To date there are

very few documented examples of localised plant extinctions that can be attributed to Allee effects. Small populations have been observed to produce zero seed [e.g. *Banksia goodii* (Lamont *et al.*, 1993)], but this does not necessarily reflect the lifetime fitness of individuals. Groom (1998) reported 28 *Clarkia concinna* patch extinctions from a total of 211 patches over a five-year period. Catastrophic disturbance accounted for more than half of these extinctions, with nine of the remaining twelve being populations known to have had low reproductive success (cause of extinction for the remaining three populations could not be determined). All recorded extinctions were of small and isolated populations. These data demonstrate that small and isolated patches have greater risk of extinction but at best provide only weak support for pollination failure as the principal causal mechanism.

Populations that are limited by factors other than the availability of seed are unlikely to be impacted by moderately depressed seed production. Density-dependent seed or seedling mortality has been reported for several tropical trees (Silander, 1978; Harms *et al.*, 2000) for which reduced seed set may have little significance for recruitment. Of course, recruitment of many other species is strongly seed limited (Eriksson & Ehrlén, 1992; Turnbull, Crawley & Rees, 2000), including many endangered native annual forbs of Californian grasslands (Seabloom *et al.*, 2003). Factors that limit recruitment are expected to change as populations grow or decline, and the importance of intraspecific competition for microsites is expected to diminish with decreasing population size (or density) to a point where seed limitation may occur. Thus even typically microsite-limited species may become seed limited when individuals are spatially dispersed, and it is exactly these populations that may be subject to Allee effects on seed production.

We should be wary of attributing too much weight to the results of short-term studies. Although there is mounting evidence from experimental and field studies of the importance of plant spacing to pollination success and seed set, many of these studies are conducted over only a fraction of the lifetime of the plants concerned. Conflicting results can be obtained if populations are studied over several years or from different sites (Morgan, 1999; Robertson *et al.*, 1999; Hendrix & Kyhl, 2000; Costin *et al.*, 2001). Weather conditions affect pollinator activity (Morgan, 1999; Hendrix & Kyhl, 2000) while pollinator populations often undergo marked and largely unpredictable fluctuations from one year to the next (Roubik, 2001). Additionally, plant productivity may in some years be subject to environmental stresses that overwhelm underlying associations of seed production with individual abundance or density (Morgan, 1999). It is the lifetime fitness of plants that is relevant when considering the implications of Allee effects for plant conservation. A sequence of years of low seed production may have little significance over the lifetime of long-lived perennials such as trees. Long-term persistence also permits trees to 'weather the storm' until conditions more favourable to seed production are re-established. Thus annuals and short-lived perennials may be more vulnerable to catastrophic decline or extinction through Allee effects, and

short-term studies that demonstrate such effects are more likely to be representative of lifetime fitness in these relatively short-lived plants.

Finally, the different elements of spatial distribution and local abundance have quantitatively and qualitatively different effects on the interactions of plants with their pollinators or seed dispersers. It is imperative, therefore, that future studies separate, in as much as it is possible to do so, the effects of population size, local density and purity, and patch isolation on plant reproductive ecology. Only in this way will we be able to determine which of these elements contributes greatest explanatory and predictive power to inform conservation and management strategies.

IX. CONCLUSIONS

(1) Pollination studies have usually been conducted on populations at high density and as a result early reviews emphasised the role of resource limitation of reproduction. More recently, attention has shifted to fragmented or sparse populations, anthropogenically derived and natural, where pollen-limited seed set subject to Allee effects has been widely noted. Declining reproductive efficiency associated with reduced densities, increased isolation among patches and, to a lesser extent, small population sizes, may lead to positive feedbacks that drive sparse populations to extinction. Furthermore, the various elements of spatial distribution and abundance can have quite different effects on patterns of pollinator behaviours over several scales from individual plants up to fragments scattered across a landscape.

(2) Plant species' vulnerabilities to Allee effects are also highly variable and based on a complex composite of life-history and breeding system characteristics. Populations of short-lived self-incompatible perennials and annuals are particularly vulnerable to Allee effects as failure to achieve full reproductive potential cannot be turned into increased investment in vegetative tissue and cannot be rescued by subsequent reproductive events. On the other hand self-compatibility, generalist pollination systems, iteroparity, long life-span and clonal growth provide buffers to temporary declines in pollinator visitation.

(3) It seems unlikely that long-lived perennials could be driven to extinction by Allee effects alone except in the most severe cases of population decline. Nevertheless, population recovery could be slowed while consecutive years of low seed production present an opportunity for competitors to establish. As many plant species in the tropics are undergoing population decline and fragmentation, Allee effects on seed production are likely to become increasingly relevant to plant species conservation.

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