

# The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence

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## ABSTRACT

Animal-mediated pollination is essential for both ecosystem services and conservation of global biodiversity, but a growing body of work reveals that it is negatively affected by anthropogenic disturbance. Landscape-scale disturbance results in two often inter-related processes: (1) habitat loss, (2) disruptions of habitat configuration (i.e. fragmentation). Understanding the relative effects of such processes is critical in designing effective management strategies to limit pollination and pollinator decline. We reviewed existing published work from 1989 to 2009 and found that only six of 303 studies considering the influence of landscape context on pollination separated the effects of habitat loss from fragmentation. We provide a synthesis of the current landscape, behavioural, and pollination ecology literature in order to present preliminary multiple working hypotheses explaining how these two landscape processes might independently influence pollination dynamics. Landscape disturbance primarily influences three components of pollination interactions: pollinator density, movement, and plant demography. We argue that effects of habitat loss on each of these components are likely to differ substantially from the effects of fragmentation, which is likely to be more complex and may influence each pollination component in contrasting ways. The interdependency between plants and animals inherent to pollination systems also has the possibility to drive cumulative effects of fragmentation, initiating negative feedback loops between animals and the plants they pollinate. Alternatively, due to their asymmetrical structure, pollination networks may be relatively robust to fragmentation. Despite the potential importance of independent effects of habitat fragmentation, its effects on pollination remain largely untested. We postulate that variation across studies in the effects of ‘fragmentation’ owes much to artifacts of the sampling regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss, and (2) mis-matches in spatial scale between landscapes studied and the ecological processes of interest. The field of landscape pollination ecology could be greatly advanced through the consideration and quantification of the matrix, landscape functional connectivity, and pollinator movement behaviour in response to these elements. Studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines, implementing effective conservation measures, and optimizing ecosystem services in complex landscapes.

*Key words:* behavioural ecology, conservation, habitat fragmentation, habitat loss, landscape ecology, pollination ecology, pollinator movement, species interactions.

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## I. INTRODUCTION

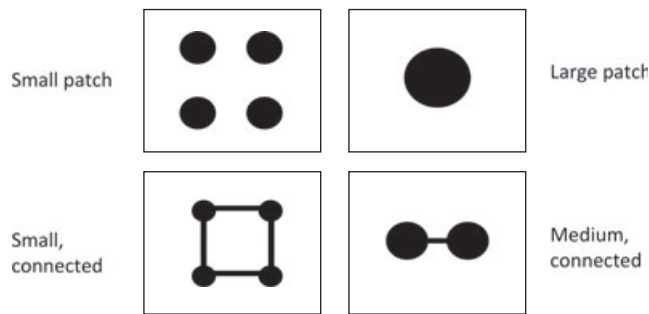
Most plant species depend on animal-mediated pollen flow (Ghazoul, 2005) in order to enhance the directedness of pollen transfer among stationary flowers (Levin & Kerster, 1969). Effective animal pollination is, therefore, extremely important for both ecosystem services [e.g. food production, medicine, carbon sequestration, flood control (Klein *et al.*, 2007; Millennium Ecosystem Assessment, 2005; Olschewski *et al.*, 2006; Potts *et al.*, 2010; Winfree *et al.*, 2008)], and for conservation of global biodiversity, independent of human uses (Bodin *et al.*, 2006; Spira, 2001). Despite the lack of direct causal links, research showing large-scale parallel declines of plants and pollinators underscores the concern that pollination as a critical ecosystem function is at risk (Biesmeijer *et al.*, 2006). Decreases in pollination and subsequent reduced plant fecundity are considered an early step in the demographic collapse of plant populations (Aizen, Ashworth & Galetto, 2002; Nason & Hamrick, 1997).

One prominent hypothesis is that such pollination declines are at least partly a function of processes occurring at larger, landscape scales (Ghazoul, 2005; Kearns, Inouye & Waser, 1998; Kremen *et al.*, 2007). This hypothesis has recently stimulated the synthesis of two previously discrete fields in ecology: landscape ecology (Turner, 1989) and pollination ecology (Müller, 1883). Over the past decade, there has been an explosion of research that tests for the effects of landscape attributes on pollination dynamics (Steffan-Dewenter & Westphal, 2008). Two recent meta-analyses revealed strong support for larger-scale drivers of pollination dynamics across multiple ecological systems and plant life-history traits (Aguilar *et al.*, 2006; Eckert *et al.*, 2010). However, the mechanisms behind such effects are unclear; little is known about which landscape attributes (e.g. habitat amount, connectivity, patch size) or what components of the pollination system (e.g. pollinator density or movement, plant demography) drive frequently observed pollination failure.

We argue that understanding such mechanisms is essential for testing ecological theory and for optimizing landscape design to deliver pollination services.

## II. LANDSCAPE COMPOSITION *VERSUS* CONFIGURATION

Landscape structure is defined by two major elements: composition and configuration (Turner, 1989). Landscape composition is the type and amount of habitat or cover types within a landscape; therefore 'habitat loss' alters landscape composition. Landscape configuration reflects the spatial pattern or 'fragmentation' of landscape elements. Fragmentation *per se* refers to the spatial configuration of remaining habitat, independent of the amount of habitat within the landscape (Fahrig, 2003). For instance, the degree to which patches within a landscape are connected by woodland corridors (Haddad, 2008), or the size of patches themselves (Bender, Contreras & Fahrig, 1998) are both aspects of landscape configuration (Fig. 1). Together, habitat loss and fragmentation are considered the primary threats to biodiversity worldwide (Pimm & Raven, 2000). The importance of distinguishing between these two aspects of landscape structure is fundamental to metapopulation dynamics theory (Hanski & Ovaskainen, 2000), reserve design and conservation of biodiversity in managed landscapes (Lindenmayer & Fischer, 2007). Some theoretical models have revealed strong influences of configuration (i.e. patch size and connectivity) on rates of local extinction and subsequent population viability (Hanski, 1998; With, Gardner & Turner, 1997). Therefore, management efforts at maintaining biodiversity have often focused on minimizing the effects of fragmentation (Saunders, Hobbs & Margules, 1991). Nevertheless, empirical support for influences of configuration on species distributions or demography is rare (Betts *et al.*, 2006). This is in striking contrast to the nearly unequivocal support for the negative influences of landscape



**Fig. 1.** Examples of four possible landscape configurations with the same total amount of habitat, but with varying spatial configuration (patch size, connectivity). Depending on life history and ecological characteristics of plants and pollinators, each configuration could have dramatically different consequences for pollination dynamics.

composition, particularly habitat loss, on biodiversity (Fahrig, 2003).

However, it appears that the lack of evidence for negative consequences of fragmentation is less due to evidence of absence than to the absence of evidence; there is a dearth of well-designed studies testing for the influence of fragmentation. In a landmark paper, Fahrig (2003) highlighted a fundamental problem in previous landscape ecological research testing for ‘fragmentation effects’; in nature, landscape configuration and composition are usually confounded. That is, landscapes with large amounts of habitat are unfragmented while landscapes with low amounts of habitat also have small, unconnected patches. Only studies that separate these confounding effects statistically (McGarigal & McComb, 1995; Trzcinski, Fahrig & Merriam, 1999) or through experimental design (Betts *et al.*, 2006; Tewksbury *et al.*, 2002) can draw inferences about the independent effects of fragmentation. As of 2003 only three studies had successfully accomplished this task, and the problem is still relatively common in the landscape ecology literature (Lindenmayer & Fischer, 2007). This is clearly problematic in terms of testing conflicting ecological theory regarding the relative importance of fragmentation and habitat loss. Indeed, debate over the relative importance of these landscape components has maintained a divide between the fields of landscape ecology and metapopulation biology (Hanski, Saastamoinen & Ovaskainen, 2006), the former minimizing the importance of landscape pattern (Fahrig, 2001, 2002; Prugh *et al.*, 2008), the latter holding pattern to be a fundamental predictor of population dynamics (Hanski, 1998). This is also an important quandary for conservation biologists who need to know which aspects of landscape structure to emphasize in reserve design and management (Collinge, 1996). Why, if fragmentation and habitat loss are usually confounded in nature, is it of management interest to determine the independent effects of these variables? Though land use is often opportunistic and haphazard, across multiple biomes, policy tools exist or are being developed to enable detailed land-use planning toward conservation biology objectives

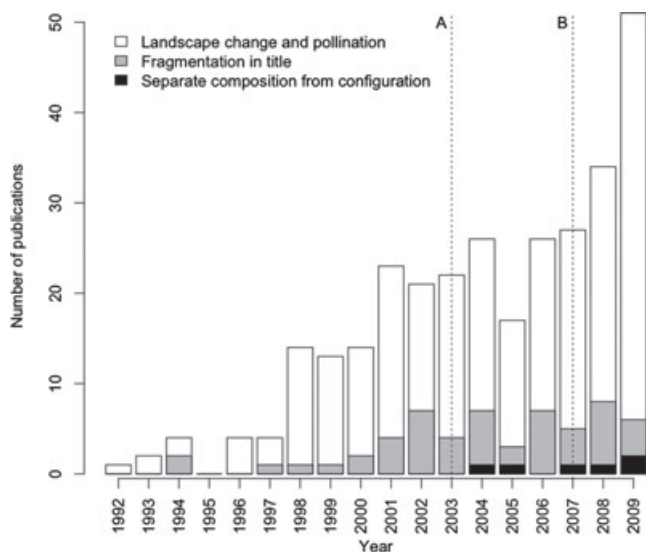
(Kremen *et al.*, 2008; Moilanen *et al.*, 2005; Smith *et al.*, 2010; Thomson *et al.*, 2009); such planning provides the opportunity to generate landscape configurations that do not typically occur as part of the normal trajectory of human disturbance, but that are potentially beneficial to the conservation of biodiversity and/or ecosystem services.

Our first objective is to determine the degree to which the fragmentation hypothesis has been tested in the pollination literature. Here, we synthesize the existing work concerning the relative effects of habitat fragmentation (landscape configuration) and habitat loss (landscape composition) on pollination. We also provide a synthesis of the current landscape, behavioural, and pollination ecology literature, to present preliminary multiple working hypotheses for explaining how these two landscape processes might influence pollination dynamics. By highlighting important knowledge gaps and pointing out promising new avenues of research we hope to assist the continued development of landscape pollination ecology.

### III. PUBLICATION HISTORY OF THE EFFECTS OF FRAGMENTATION ON POLLINATION

A substantial body of published work has focused on the effects of ‘‘habitat fragmentation’’ on plant reproduction, particularly pollination. To examine the current knowledge we conducted a search of the *ISI Web of Science* database. We searched for articles containing ‘‘frag\*’’ and ‘‘poll\*’’ in the topic field (Topic=[frag\* AND poll\*], Timespan=1970-2009, Databases=SCI-EXPANDED, SSCI) and ‘‘Ecology’’ as a subject area option. This resulted in a list of 761 articles. While this is not an exhaustive list, we consider it to represent an unbiased sample of the existing literature. From these, we selected all of the articles examining the effects of landscape variables [both composition (e.g. habitat amount, habitat quality, matrix quality) and configuration (e.g. patch size, isolation, edge)] on plant pollination, fecundity or genetics. We also included articles examining the effects of landscape disturbance on pollinator demography or behaviour. We conducted a detailed examination of the resulting 303 articles (see online supporting information Appendix S1) dealing with the effects of landscape disturbance on pollination systems. We considered a study to have examined independent effects of habitat loss and habitat fragmentation if the authors (1) controlled for habitat amount statistically, or (2) applied mensurative or manipulative experiments (*sensu* Hurlbert, 1984). Statistical control constitutes including both habitat loss and fragmentation as predictor variables within the same multiple-regression model. Manipulative and mensurative experiments successfully disentangle habitat loss from fragmentation when these variables are independently varied using an *a priori* experimental design.

Since the publication of the first papers investigating landscape disturbance on pollination dynamics in the



**Fig. 2.** The number of articles published on the supposed ‘effects of habitat fragmentation’ in pollination systems divided into those failing to separate the effects of habitat loss from habitat fragmentation (white bars) and those studies properly separating the effects of habitat fragmentation (black bars). Grey bars show articles including ‘fragmentation’ in the title. Dotted vertical lines represent publication of key papers by (A) Fahrig (2003) and (B) Lindenmayer & Fischer (2007) stressing the importance of separating composition from configuration.

early 1990s the field of landscape pollination ecology has grown rapidly (Fig. 2) and this growth is expected to increase (Millennium Ecosystem Assessment, 2005; Natural Environment Research Council, 2010). Of the 303 papers examining the effects of landscape disturbance on plant pollination services, 182 discussed their results as being the effects of habitat fragmentation. Fifty-eight included

habitat fragmentation in their title. Studies often examined multiple combinations of landscape metrics and response variables (results are summarized in Table 1). While many of these articles measured configuration metrics (e.g. patch size, isolation, edge), only five empirical studies and one simulation study examined the independent effects of habitat configuration (Table 2). All others did not distinguish changes in landscape configuration from those of composition.

Unfortunately, these results provide strong evidence that though there has been great progress in testing for the influence of landscape-level changes on pollination success (e.g. Aguilar *et al.*, 2006), the landscape pollination ecology literature has not yet effectively distinguished between the effects of landscape configuration and composition (Fig. 2). This is despite the fact that titles of articles imply that aspects of configuration have been tested (e.g. ‘Effects of fragmentation on pollination...’). Indeed, reviews and meta-analyses of the effects of landscape structure on pollination have generally implied that fragmentation has large negative effects on plant pollination (e.g. Aguilar *et al.*, 2006; Ashworth *et al.*, 2004). This confusion over the term ‘fragmentation’ prevalent in pollination ecology supports Fahrig’s (2003) and Lindenmayer & Fischer’s (2007) reviews of research on habitat fragmentation and biodiversity. Interestingly, these two key studies in landscape ecology (cited 676 and 30 times, respectively) appear to have had little effect in terms of stimulating research that separates landscape-scale drivers of pollination (Fig. 2). This does not detract from the importance of existing studies; the repeated finding that ‘landscape structure’ has strong influences on pollination (Aguilar *et al.*, 2006) and pollinators (Winfree *et al.*, 2009) is of critical importance. However, the question of which components of landscape structure are driving declines in pollination remains largely unanswered.

**Table 1.** Summary of 303 articles examining the effects of landscape changes on pollination systems. Entries represent the number of times articles have attempted to investigate the given combination of variables. Each study may contain more than one metric and response variable. Reviews were excluded. The number of instances where configuration effects were successfully examined independent of composition is shown in bold

| Landscape metrics                        | Response variables |                      |               |                        |                       |                                     |                          |                           |                          |
|--|--------------------|----------------------|---------------|------------------------|-----------------------|-------------------------------------|--------------------------|---------------------------|--------------------------|
|  | Pollination (70)   | Pollen movement (13) | Seed set (67) | Genetic diversity (45) | Visitation rates (31) | Pollinator abundance/diversity (44) | Pollinator movement (16) | Pollinator diet shift (5) | Pollination syndrome (3) |
| Habitat loss (33)                        | 12                 | 0                    | 5             | 4                      | 5                     | 14                                  | 1                        | 2                         | 1                        |
| Patch size (102)                         | 31                 | 2                    | 40            | 16                     | 17 (2)                | 14 (1)                              | 1                        | 2                         | 1                        |
| Isolation (90)                           | 28                 | 7                    | 23 (1)        | 25                     | 11 (2)                | 14 (2)                              | 2                        | 1                         | 1                        |
| Corridors (3)                            | 1                  | 2 (1)                | 0             | 0                      | 0                     | 0                                   | 2                        | 0                         | 0                        |
| Edge (13)                                | 3                  | 0                    | 3             | 0                      | 1                     | 7                                   | 2                        | 0                         | 0                        |
| Matrix quality (8)                       | 0                  | 0                    | 1             | 2                      | 2                     | 2                                   | 2                        | 0                         | 0                        |
| Habitat degradation (19)                 | 6                  | 0                    | 4             | 2                      | 4                     | 4                                   | 1                        | 1                         | 0                        |
| Disturbed <i>versus</i> undisturbed (30) | 6                  | 4                    | 6             | 6                      | 2                     | 6                                   | 5                        | 0                         | 1                        |



Table 2. Details of the five empirical studies examining the independent effects of configuration on pollination systems. (-), negative effects of fragmentation; ns, no significant effect; na, not available. Terminology used in the actual studies was revised for consistency and to reflect the most commonly accepted term for each landscape metric

| Study                             | Configuration metric/response variable | Effect | Pollinator       | Region    | Landscape size (ha) | Separation method       |
|-----------------------------------|--|--------|------------------|-----------|---------------------|-------------------------|
| Cresswell & Osborne (2004)        | Patch size/visitation rates            | (-)    | bees             | temperate | 3.38                | manipulative experiment |
| Townsend & Levey (2005)           | Isolation/visitation rates             | ns     |                  |           |                     |                         |
|                                   | Corridors/pollen movement              | (-)    | bees/butterflies | temperate | 40.72               | manipulative experiment |
| Diekotter <i>et al.</i> (2007)    | Patch size/seed set                    | ns     | bees/butterflies | temperate | 0.02                | manipulative experiment |
| Steffan-Dewenter & Schiele (2008) | Patch size/visitation rates            | ns     |                  |           |                     |                         |
|                                   | Patch size/pollinator abundance        | (-)    | bees             | temperate | na                  | statistical             |
| Farwig <i>et al.</i> (2009)       | Isolation/seed set                     | (-)    | flies/bees       | temperate | 78.54               | mensurative experiment  |
|                                   | Isolation/visitation rates             | ns     |                  |           |                     |                         |

#### IV. THE IMPORTANCE OF LANDSCAPE DISTURBANCE IN POLLINATION SYSTEMS

Pollination networks have been argued to be relatively robust and resilient to environmental perturbation (Bascompte, Jordano & Olesen, 2006); if a plant species depends strongly on an animal species, the animal depends weakly on the plant and overall, the number of strong dependencies is low. This observed asymmetry of pollination networks at the community level (Bascompte *et al.*, 2006; Memmott, Waser & Price, 2004) is thought to ‘buffer’ against landscape changes to some degree. However, declines in pollination success as a function of landscape disturbance (e.g. Aguilar *et al.*, 2006; Kremen *et al.*, 2004; Kremen, Williams & Thorp, 2002) along with correlated negative responses by multiple species of native bees to increasing amounts of intensive agriculture (Winfree & Kremen, 2009), suggest that aspects of highly altered landscapes are impacting pollination despite mutualistic network structures that promote robustness. Meta-analyses suggest that these landscape-mediated pollination declines are driven primarily through ‘pollen limitation’ (i.e. insufficient pollen delivery in disturbed areas; Aguilar *et al.*, 2006) and/or reduced ‘outcrossing rates’ (i.e. lowered rates of pollen delivery from unrelated individuals; Eckert *et al.*, 2010). However, the specific mechanisms behind reduced pollen quantity and/or quality are not well known (Eckert *et al.*, 2010).

Animal-mediated pollination is a complex process by which plants capitalize on the mobility of their associated pollinators to reproduce sexually. Successful pollination depends on many interacting factors (e.g. number of flowers, distance between plants, number of pollinators, pollinator movement, pollinator diet breadth, phenology, pollen quantity *versus* quality, etc.; Ghazoul, 2005; Kremen *et al.*, 2007). Landscape disturbance may influence pollination *via* altering three primary mechanisms: (1) plant density, (2) pollinator density, and (3) pollinator

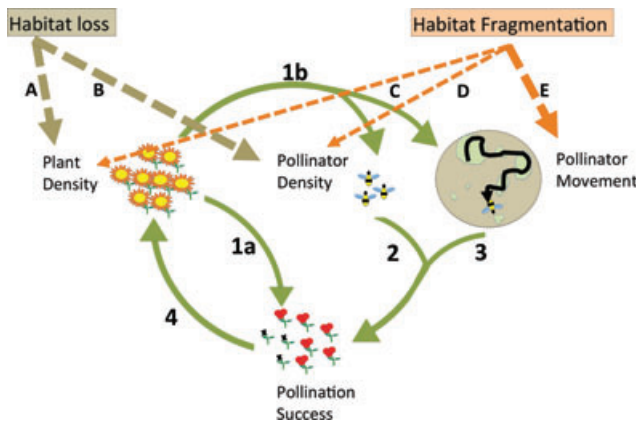
behaviour (particularly movement). To facilitate uncovering the mechanisms behind pollination declines in disturbed landscapes, we briefly review the importance of these three primary mechanisms to pollination success (for more general discussion see: Ghazoul, 2005; Kremen *et al.*, 2007) and examine the potential for habitat loss and fragmentation to influence each component directly (Fig. 3).

##### (1) Plant density

A change in the abundance, distribution or health of plants has the potential to influence pollination. Pollination success is related to both the number of conspecific flowers nearby (Ellstrand & Elam, 1993; Feinsinger *et al.*, 1986; Kunin, 1997; Menges, 1995; Waites & Agren, 2004) and the distance between flowers within a patch (Bosch & Waser, 1999, 2001). Plant health is important since it influences the size, number and quality of flowers which, in turn, is key for enhancing a plant’s attractiveness to pollinators (Caruso, Remington & Ostergren, 2005). Changes in the surrounding plant community also affect interspecific competition for pollination (Caruso, 1999; Chittka & Schurkens, 2001; Levin & Anderson, 1970). Plant density should be considered at multiple scales since it encompasses density of plants within patches, density of patches containing plants, and density of plant populations, all of which could influence plant and pollinator demography and pollinator behaviour.

##### (2) Pollinator density

The availability of pollinators in a landscape has a substantial impact on pollination systems. Both the abundance (Lennartsson, 2002) and diversity of the pollinator community (Donaldson *et al.*, 2002; Klein, Steffan-Dewenter & Tschardtke, 2003; Vázquez, Morris & Jordano, 2005) have been found to predict pollination success. Landscape changes that increase or decrease the availability of pollinators could



**Fig. 3.** Conceptual model of the feedback loops involving the major components of pollination and the effects of habitat loss and fragmentation on each component. Dotted arrow thickness represents hypothesized effect strength. (1a) Plant densities directly affect pollination rates; reduced densities likely decrease pollen availability and therefore the likelihood of pollen transfer. (1b) Plant densities affect both pollinator densities, *via* behavioural and demographic processes, and pollinator movements. Pollinator densities (2) and pollinator movements (3) influence pollination success. Over the longer term, pollination success subsequently drives plant densities (4). Habitat loss can directly decrease plant (A) and pollinator (B) densities. Habitat fragmentation may increase or decrease plant (C) and pollinator (D) densities and also has been shown to influence pollinator movements (E). One hypothesis is that the number of different points where habitat loss and fragmentation may influence pollination systems, combined with the potential for feedback loops, may result in pollination services displaying high sensitivity to landscape changes.

subsequently influence the effectiveness of the pollination systems involved.

### (3) Pollinator behaviour

The availability of pollinators in a landscape or region does not ensure pollination. The effectiveness of available pollinators at pollen transfer depends on pollinator behaviour. Changes in pollinator daily movements, including foraging extent (area covered in search of resources) and foraging pattern influence how pollen is distributed across the landscape (Kremen *et al.*, 2007). Pollen can only be distributed along the movement paths of its pollen vectors, so areas left unvisited will clearly remain unpollinated. Conversely, areas that are frequented more often or situated in high-traffic regions may receive higher rates of pollination (Tewksbury *et al.*, 2002) and visit frequency appears to be a good predictor of pollination success (Jennersten, 1988; Vázquez *et al.*, 2005).

Pollinator foraging strategy is also a critical behaviour since floral-specialist pollinators typically deliver higher quality ‘pure’ conspecific pollen loads (Ashman *et al.*, 2004; Levin & Anderson, 1970). Floral-generalist pollinators typically transport mixed pollen from several species and deliver

larger amounts of incompatible pollen. This has been shown to block stamens and limit seed set (Brown & Mitchell, 2001). Pollen loads can be further decreased when pollinators visit many different flower species within a foraging bout; conspecific pollen may be scraped from pollinators by the floral architecture of heterospecifics (Levin & Anderson, 1970; Murcia & Feinsinger, 1996). The presence of co-flowering plant species may also reduce pollination success by resulting in competition among different flower species for limited pollinator visits, thereby decreasing the delivery of species-specific pollen (Bell, Karron & Mitchell, 2005; Chittka & Schurkens, 2001; Levin & Anderson, 1970). This is particularly relevant as pollinator diet breadth is often context dependent; pollinators have been shown to switch from floral specialist to generalist strategies (or *vice versa*) depending on resource availability (Chittka & Schurkens, 2001; Fontaine, Collin & Dajoz, 2008; Smithson & MacNair, 1997). Such diet shifts can result in changes in visitation rates to competing plant species, individual inflorescences or individual flowers, all of which can significantly impact pollination success and have genetic consequences to plant populations (Ghazoul, 2005).

## V. EFFECTS OF HABITAT LOSS

The hypothesized negative effect of habitat loss on the first two mechanisms outlined above—plant and pollinator density—is relatively straightforward under most circumstances. Reducing the amount of habitat in the landscape (e.g. through land clearing) decreases conspecific plant density at the landscape scale. The negative effects of habitat loss on plant abundance, species richness and population size have been well documented (Bascompte & Rodriguez, 2001; Duffy, 2003; Harpole & Tilman, 2007; Helm, Hanski & Partel, 2006; Laurance, Gascon & Rankin-de Merona, 1999; Lindborg & Eriksson, 2004; Vellend, 2003). Fewer plants results in reduced pollen availability in the system and more limited options for outcrossing. A reduction in effective population size lowers the number of pollen donors or receivers as well as the quantity of resources available to pollinators.

Similarly, habitat loss has been shown to have strong negative effects on pollinator abundance (Sjodin, Bengtsson & Ekbom, 2008; Steffan-Dewenter & Schiele, 2008; Taki, Kevan & Ascher, 2007; Winfree *et al.*, 2009). Therefore, in most instances, habitat loss will reduce numbers of both plants and pollinators (see A and B in Fig. 3). This results in lower pollen availability and fewer vectors to move pollen through the landscape. Both of these mechanisms will likely reduce pollination success, particularly if the simultaneous reduction of many species overwhelms the buffering capacity of the pollinator network structure (Winfree & Kremen, 2009).

In practice, because ‘habitat loss’ often occurs simultaneously with ‘fragmentation’, under some conditions its effects may be more complex than described above. Below, as a guide to future research, we provide some preliminary

hypotheses for how the independent effects of fragmentation might influence pollination.

## VI. EFFECTS OF FRAGMENTATION

Given the absence of published work specifically devoted to the influence of habitat fragmentation *per se* on pollinators and pollination, we found it necessary to turn to broader research on the effects of landscape configuration on plants, animals, and animal behaviour. Though this work is not specific to pollination, we expect that the processes driving fragmentation effects on plants and animals generally are likely to be pertinent to pollination systems.

### (1) Plant and pollinator densities

The effects of habitat fragmentation on plant and animal distributions are hypothesized to occur primarily as a result of alteration to three aspects of landscape configuration: patch size, edge, and landscape connectivity (Bender *et al.*, 1998; Bolger *et al.*, 2000; Tewksbury *et al.*, 2002). The effects of patch size are expected to influence demographic (Lande, 1993) and genetic stochasticity (Whitlock, 2004), local extinction (Hanski & Ovaskainen, 2000), establishment (Bowman, Cappuccino & Fahrig, 2002), habitat selection (Fletcher & Hutto, 2008), animal predation of pollinators (Batory & Baldi, 2004), resource quality (Burke & Nol, 1998), and interspecific competition (MacArthur, Diamond & Karr, 1972). Edge effects in plant and animal communities are common (Chen, Franklin & Spies, 1992; Murcia, 1995), but may be positive (Chen *et al.*, 1992) or negative (Bruna, 2002) and affect distributions, abundance (Bolger *et al.*, 2000), growth (McDonald & Urban, 2004), and reproduction (Burgess *et al.*, 2006). Edge effects have been found to occur as a function of local micro-climatic influences (Murcia, 1995) and elevated animal predation (Cantrell, Cosner & Fagan, 2001). A third component of landscape configuration, connectivity, has been found to affect rates of animal movement (see Section VI.2a) and therefore rates of dispersal and patch colonization (Haddad, 2000).

Research on metapopulations has revealed the potential importance of landscape configuration to plant and animal population dynamics (Hanski & Ovaskainen, 2000). Metapopulation ecology involves the study of discreet sub-populations occupying habitat patches within an unsuitable matrix (Levins, 1969). Under equilibrium conditions, metapopulations are maintained *via* interaction among the sub-populations through individual dispersal. This approach to population dynamics emphasizes the importance of characteristics of populations that affect extinction (e.g. patch size) and dispersal rates (e.g. distance among patches) (Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2004). Metapopulation theory is particularly relevant to pollination dynamics in disturbed areas where interactions between plants distributed among patches is maintained primarily through pollinator movement. In addition, metapopulation

models have been used to demonstrate the effects of patch size and connectivity on insect populations, many of which are pollinators (Hanski *et al.*, 2006; Wahlberg, Klemetti & Hanski, 2002a; Wahlberg *et al.*, 2002b). Unfortunately, one legacy of early metapopulation approaches and the Theory of Island Biogeography (MacArthur & Wilson, 1967) has been the adoption of a dichotomous ‘patch’ (i.e. habitat) and ‘matrix’ (i.e. non-habitat) view of terrestrial landscapes that are usually far more complex (Fahrig *et al.*, 2010); although some pollinators may be organized as metapopulations, distributions and movements may not correspond well to structurally defined patch/matrix delineations (Fischer & Lindenmayer, 2006) and move readily across—and even use resources within—what may be expected as ‘non-habitat’ by the researcher (see Section VII).

Independent effects of habitat fragmentation on population density or distributions have been demonstrated empirically for several taxa including plants (Brudvig *et al.*, 2009; Damschen *et al.*, 2008), insects (Collinge & Forman, 1998; Krawchuk & Taylor, 2003; With *et al.*, 2002), birds (Betts, Forbes & Diamond, 2007; Betts *et al.*, 2006) and mammals (Collins & Barrett, 1997). This suggests that independent effects of fragmentation on plant and pollinator densities may occur in many systems and taxa. Unfortunately, due to the paucity of studies on this topic, the generality and strength of these findings is debated (Prugh *et al.*, 2008) and still not well understood.

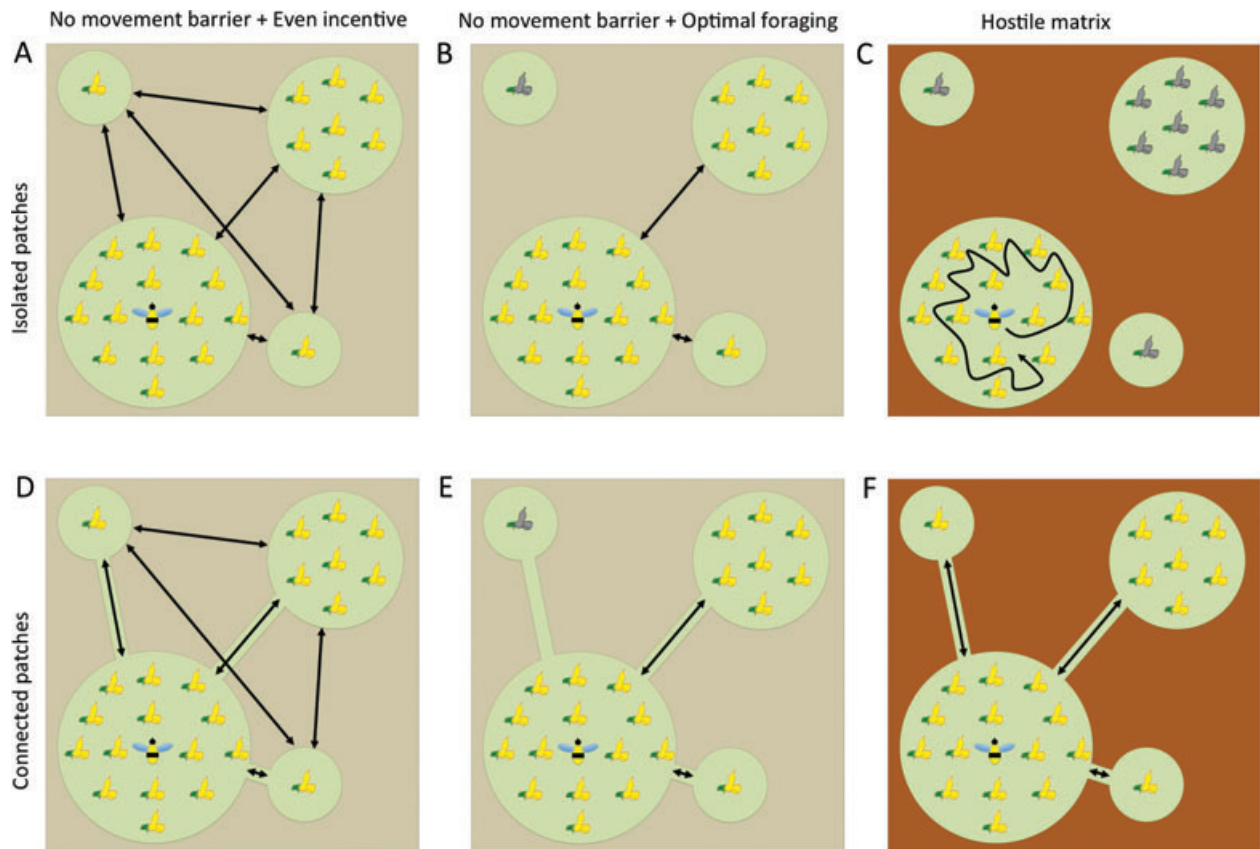
### (2) Pollinator behaviour

We anticipate that some of the most intriguing possibilities for independent fragmentation effects on pollination may stem from a third potential mechanism, ‘pollinator behaviour’ (see E in Fig. 3). Such responses to fragmentation are likely mediated *via* changes in both pollinator movement and diet selection.

#### (a) Movement effects

Optimal foraging theory suggests that animals should forage in such a way as to maximize their energy intake per unit time (MacArthur & Pianka, 1966). While the majority of existing work on animal movement has been conducted on vertebrate species for logistical reasons, we expect invertebrates to show similar behavioural responses at relevant scales. Movements between patches presumably have a cost; time is spent traveling which could otherwise be spent procuring resources (Hinsley, 2000). Visiting small patches will be less profitable, particularly if inter-patch distance increases (Tentelier, Desouhant & Fauvergue, 2006). These gap-crossing movements may also be risky and increase exposure to predation (Lima & Zollner, 1996). For a variety of animals, including birds (Bélisle & Desrochers, 2002) and mammals (Bakker & Van Vuren, 2004), gap crossing appears to be the primary risky behaviour documented in fragmented landscapes and simulations have shown mortality occurring during movements between patches to be a major factor in population survival (Bender & Fahrig, 2005). Animals may





**Fig. 4.** Schematic diagrams of the effects of matrix quality, incentive strength and connectivity on pollination. Suitable habitat (assumed to be the same for both the plant and pollinator) is shown in green with matrix types shown as either grey (no barrier to movement) or brown (extreme barrier to movement). Plants visited by pollinators are shown in yellow and unvisited plants are grey. Arrows represent pollinator movements. Panels A–C represent unconnected landscapes and D–F represent landscapes with patches connected by corridors. All landscapes have the same total amount of habitat. (A) Habitat patches are separated by a matrix that imposes no barrier to pollinator movement and the pollinator has even incentive to visit each patch because there is no cost to movement (i.e. pollinators move freely among all patches in the landscape). (B) Matrix imposes no barrier to movement, but pollinators make decisions according to optimal foraging. Pollinators visit patches according to distance/incentive trade-offs avoiding small remote patches. (C) Patches are imbedded in a ‘hostile matrix’ which prevents pollinator movement. The pollinator remains within a single patch. (D) Patches are connected by corridors, but the matrix imposes no barrier to movement and pollinators treat each patch as even incentive. Pollinators move between all patches as in A independently of actual habitat connections. Corridors play only a very limited role in situations with a highly permeable matrix. (E) Patches are connected, but pollinators make decisions according to optimal foraging. Movement trade-offs are the same as in B. (F) Patches are connected by corridors within a hostile matrix. Pollinators move along the corridors between patches. For graphical simplicity the matrix permeability we use here is artificially dichotomous (see Section VII). Complex interactions between pollinator behaviour, landscape pattern, and matrix permeability are predicted to have strong implications for the importance of landscape fragmentation to pollination dynamics.

choose to cross small gaps, but with limited regularity or may choose longer indirect routes to circumnavigate (e.g. warblers; Desrochers & Hannon, 1997; and hummingbirds; Hadley & Betts, 2009). Gaps larger than a certain size may constitute obstacles due to animal physiological limitations (Moore *et al.*, 2008) or the fact that distant resource patches are outside the organism’s perceptual range (Conradt, Roper & Thomas, 2001; Diekötter *et al.*, 2007; Lima & Zollner, 1996). Therefore, pollinators are likely influenced by both patch size and distance between patches when undertaking movement decisions. Visiting small patches will be less profitable, particularly as inter-patch distance increases (Tentelier *et al.*, 2006; Fig. 4B,C). Animal decisions regarding

resource exploitation in fragmented landscapes are thus likely to be dependent on trade-offs between resource availability and risk (Turcotte & Desrochers, 2003).

Though landscape-scale experimental studies are rare (Beier & Noss, 1998), the few existing studies have shown that corridors increase movement rates for multiple animal taxa (Haddad *et al.*, 2003). Preliminary evidence suggests that corridors or at least increased ‘functional connectivity’ - the degree to which the landscape facilitates or impedes movements between resource patches (Taylor *et al.*, 1993) - can facilitate the movements of pollinators (Haddad, 2000, 1999) and increase subsequent pollination success (Townsend & Levey, 2005; Fig. 4F).

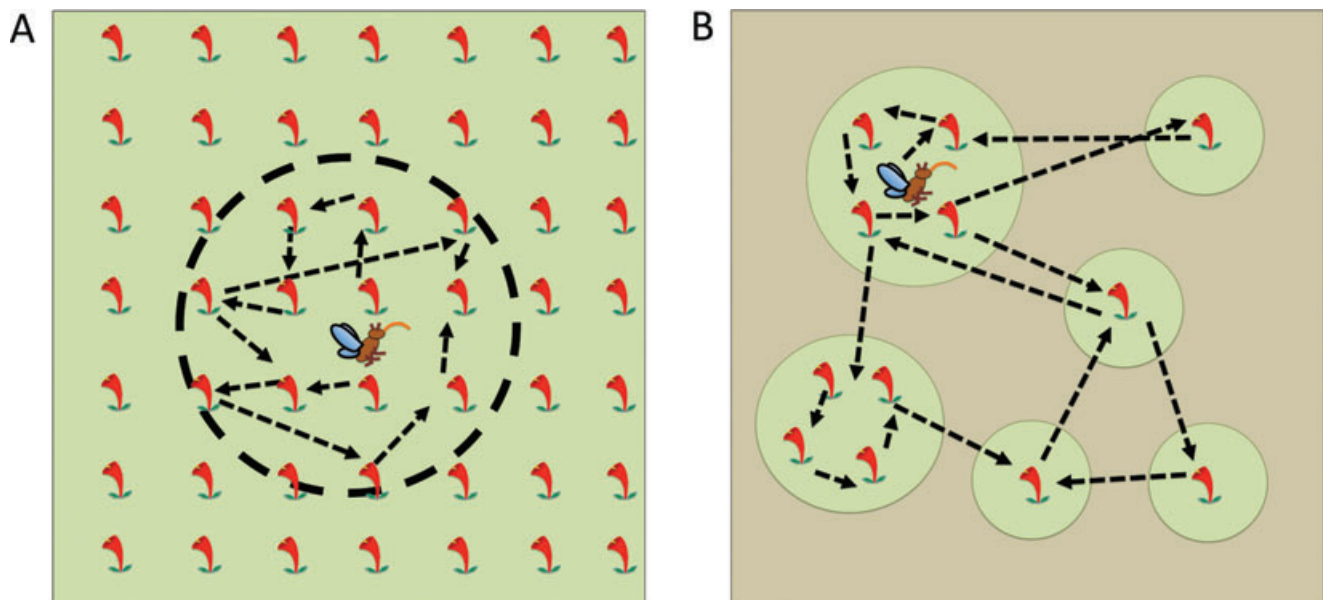


Habitat edges often have profound impacts on animal movements and if pollinators show similar responses, the pattern of edges in a landscape could have strong implications for pollen movement. Evidence exists for animals both avoiding (Dolby & Grubb, 1999) and associating with edges (Desrochers & Fortin, 2000; Hadley & Desrochers, 2008) during their daily movements. Edges may differ from interior regions in terms of predation risk (Ibarzabal & Desrochers, 2004) and their profitability (Thompson & Willson, 1978) leading to behavioural decisions to avoid these areas. Edges can also direct or channel animal movements simply by acting as a movement conduit (Desrochers & Fortin, 2000). In this manner, edges can direct the movements of an animal even deep within the patch (Desrochers & Fortin, 2000).

By altering pollinator movements, fragmentation could also facilitate pollination in certain instances. For example, Brosi, Armsworth & Daily (2008) and Keitt (2009) found that if foraging movements of pollinators are limited in Euclidian distance, landscape designs that intersperse pollinator habitat with floral resources (i.e. a highly fragmented landscape) could be preferable. Indeed, Winfree *et al.* (2008) recommended this approach to maximize crop visitation by native pollinators; they proposed forested hedgerows embedded in agricultural landscapes to facilitate crop access for solitary tree-cavity-nesting bees. Similarly, Holzschuh, Steffan-Dewenter & Tscharnkte (2008) showed that interspersions of organic crops increased native bee diversity in landscapes dominated by conventional wheat

fields. However, it is important to note that these designs represent a particular circumstance where the objective is maximization of crop pollination. While such landscape patterns may facilitate pollination of agricultural crops, they might not have similarly positive consequences for the native plants depending on these same pollinators. Interspersion of high-reward flowering crops could actually disrupt networks and reduce the availability of pollinators for native plants (Aizen, Morales & Morales, 2008). Further, such recommendations need to be placed in the context of pollinator population dynamics. If large patches have lower probabilities of pollinator extinction, as would be expected under metapopulation theory, a mix of small interspersed, and large contiguous patches might be optimal for pollination services (Brosi *et al.*, 2008).

Under some circumstances, fragmentation could also facilitate outbreeding (Heinrich & Raven, 1972). In fragmented systems with patchily distributed plants, pollen delivery from distant individuals should be more frequent when floral specialist pollinators are forced to cover larger areas to procure sufficient resources (Fig. 5). Although quantity of pollen should decrease for the reasons highlighted above (see Section IV.1), quality of pollen delivered could potentially improve due to higher amounts of outcross pollen from more distant conspecific plants (Dick, 2008). Further, in some instances, the frequency of flower visitation appears to increase in smaller patches (Diekötter *et al.*, 2007; Goulson, 2000). Visiting a smaller proportion of inflorescences as patch size increases is expected to be an optimal strategy (Goulson,



**Fig. 5.** Diagrams representing the possibility for habitat fragmentation to increase outcrossing. (A) A landscape with high plant densities. Pollinator movements among flowers are shown by dotted arrows. The total area covered by the pollinator is shown by the dashed circle. This likely results in high levels of pollen delivery, but low rates of outcrossing. (B) Pollinator movements in a fragmented landscape with lower flower densities. The pollinator is forced to travel to more remote flowers in order to procure the same quantity of resources. This results in pollen movement among distant individuals that are less likely to be related, resulting in higher rates of outcrossing. It is important to note that the scenario shown in B requires a pollinator with high vagility and habitat generalization.

2000). Provided inter-patch movement is unimpeded, such behaviour could facilitate *per capita* plant reproductive success in small patches. Such scenarios should only be possible in systems with highly mobile, habitat-generalist pollinators whose movements are unencumbered by fragmentation.

#### (b) Diet selection

Pollinator diet selection is important to pollination success since it affects the number of visits to flowers (Bell *et al.*, 2005) as well as the quality of pollen delivered (Aizen & Harder, 2007). Pollinator foraging preferences are often plastic and vary depending on the characteristics of the plant community in which they forage (Fontaine *et al.*, 2008). Introduction of invasive species (Aizen *et al.*, 2008; Chittka & Schurkens, 2001) and changes in heterospecific flower densities (Jakobsson, Lazaro & Totland, 2009) have both been shown to decrease pollination success. Since plant densities, relative flower abundance (e.g. native/invasive) and flower quality (e.g. number of inflorescences, display size) can all be affected by landscape configuration (particularly edge effects; Murcia, 1995, see Section VI.1) it follows that pollinator foraging behaviours may also be fragmentation sensitive.

Visitation rates to individual flowers have been shown to differ depending on patch size (Cresswell & Osborne, 2004) and resource density (Kunin, 1997). Flower quality is also a factor in visitation (Grindeland, Sletvold & Ims, 2005) that can vary with proximity to edge (Jules, 1998). These increases in flower abundance and quality have been hypothesized to drive higher pollinator abundances next to edges (Stouffer & Bierregaard, 1995). Therefore, we expect foraging patterns in fragmented areas with modified flowering communities to differ from behaviour in unfragmented landscapes.

Fragmentation *per se*, therefore, has the potential to influence pollination dynamics by directly affecting pollinator or plant densities and altering pollinator behaviour (movement, diet). Because plant and animal taxa might respond to landscape configuration in contrasting ways, the effects of landscape fragmentation will likely be complex.

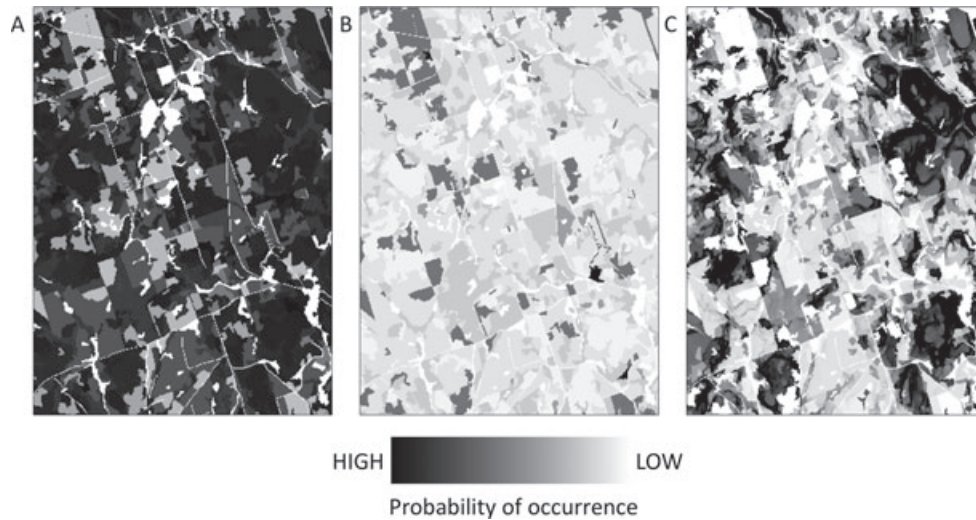
## VII. DEFINING HABITAT AND MATRIX

### (1) Habitat

Properly defining landscape elements is a critical component of landscape ecology (Wiens, 1995). In order to examine the effects of landscape disturbance on pollination it is important to quantify changes that have occurred and the characteristics of the habitats that remain. Definitions of 'habitat' are inherently species specific; attributes such as habitat amount, patch size and connectivity often differ greatly among plant or pollinator species even within the same landscape (Addicott *et al.*, 1987; Betts *et al.*, 2007; Holzschuh, Steffan-Dewenter & Tscharnke, 2010; Valdés

& García, 2009). To address this issue, the 'species-centered approach' (Fig. 6) uses species distribution models to quantify landscape elements from the perspective of individual species (Betts *et al.*, 2006). This approach has now been used to explain species occupancy and demography as a function of habitat loss and fragmentation (Betts *et al.*, 2007; Zitske, Betts & Diamond, 2011). However, applying this method is more complicated in landscape pollination ecology because plants and their associated pollinators may perceive the landscape in different ways (Cane, 2001); though it seems intuitive that habitat for a plant is also habitat for its pollinators, this is not necessarily the case. Habitat from the plant's perspective comprises the suite of different abiotic and biotic characteristics that permit their growth and reproduction at a single site (Bazzaz, 1991). Habitat from the pollinator's perspective is often more complex because each life-history requirement may necessitate different compositional and structural features occurring across multiple sites (Lima & Zollner, 1996). Foraging, breeding and movement habitats are spatially discrete for many species (Westrich, 1996). For instance many native bee pollinators nest in forest, but forage in the surrounding cropland (Ricketts, 2004; Sande *et al.*, 2009). Alternatively, some pollinators appear to have high fidelity to nesting and movement habitats that co-occur with food plants (e.g. Stiles, 1975). Regardless, it is critical that the definitions used to characterize landscapes are pertinent to the questions and organism considered (Cane, 2001). A variety of powerful tools are now available to model the distribution of plants and pollinators—even when only presence data are available (Phillips, Anderson & Schapire, 2006). Though it might seem obvious that landscapes should be quantified using an organism-based approach, we found many studies that test for the influence of landscape structure on species distributions and pollination based on landscape features that are primarily relevant to humans and/or easily measurable (e.g. amount of forest cover, distance between forest patches). Such variables do not necessarily correspond to the ecological processes themselves.

The spatial scale of research should also be justified in biological terms (e.g. Holzschuh *et al.*, 2010; Kremen *et al.*, 2002) rather than logistical constraints since choice of scale can have dramatic effects on results (Willis & Whittaker, 2002). The spatial scale of research should be relevant to both daily foraging movements and often larger-scale population dynamics of pollinators (Brosi *et al.*, 2008). Ignoring these considerations risks Type II error where it is concluded that 'fragmentation' of landscapes is irrelevant to pollination, when absence of detected effects is purely a result of incorrect initial definitions of landscape structure (Betts & Villard, 2009). For example, though they did not consider the independent effects of fragmentation, Lonsdorf *et al.* (2009) contributed an important advance by quantifying guild-specific pollinator nesting resources, floral resources and foraging distances to estimate the relative abundance of pollinators, and therefore pollination services, across agricultural landscapes. Conversely, small-scale manipulations successfully examining independent fragmentation effects (Cresswell



**Fig. 6.** Three maps showing the same geographic area from the perspective of three different hypothetical pollinator species representing (A) a habitat generalist, (B) an early-seral forest specialist, (C) a late-seral forest specialist. In each map, dark shades indicate higher pollinator densities according to a species distribution model (SDM). Habitat amount, quality, patch size and connectivity all vary greatly within the same landscape depending on the organism.

& Osborne, 2004; Diekötter *et al.*, 2007) may not reflect natural landscape disturbance levels of conservation interest or pollinator dispersal distances (Osborne *et al.*, 1999).

## (2) Matrix

The vast majority of studies we reviewed considered habitat loss and fragmentation as a dichotomous process, reflecting habitat patches as islands in a sea of uniform, unsuitable space. Though this approach facilitates easy landscape measurement, as noted above it has become increasingly clear that this view is an over-simplification in most landscapes (Jules & Shahani, 2003). The characteristics of the intervening ‘matrix’ of landscape elements separating habitat patches have the potential to influence pollinator movement among patches (Fig. 4) and the quality of the intervening matrix can either mediate or exacerbate the influence of fragmentation (Bender & Fahrig, 2005). For example, in many instances—particularly in forested or less intensively managed agricultural landscapes—distinctions between ‘patch’ and ‘matrix’ may be subtle (Fig. 6). A relatively favourable matrix may actually enhance the quality of remaining patches through increased resource availability (a process termed ‘habitat supplementation’; Dunning, Danielson & Pulliam, 1992) and may reduce movement resistance (Brotons, Mönkkönen & Martin, 2003). Matrix resistance is species specific and is a function of behavioural avoidance (Hadley & Betts, 2009), physical crossing ability (Moore *et al.*, 2008), and/or the organism’s perceptual range (Lima & Zollner, 1996). Presence of sufficient resources for foraging may also influence matrix permeability. In most systems, the matrix presents varying levels of resistance to animal movements, ranging from a complete barrier (Moore *et al.*, 2008) to offering relatively little opposition or even facilitating movement (Fig. 6A). For instance, in a small-scale

experiment, Diekötter *et al.* (2007) found that abundance of pollinators, flower visitation and seed set were higher in clover patches surrounded by bare ground than grass matrix.

Recently there has been a great deal of progress in measurement and quantification of landscape resistance to animal movement using ‘graph theoretic’ approaches. Graph theory is a body of mathematics designed to address problems of connectivity, flow and routing in networks (Adriaensen *et al.*, 2003; Urban *et al.*, 2009). Spatial graphs based on empirically derived pollinator movement resistances could be incorporated into statistical models predicting pollination success as a function of functional connectivity for pollinators (see Section VIII and Fig. 7).

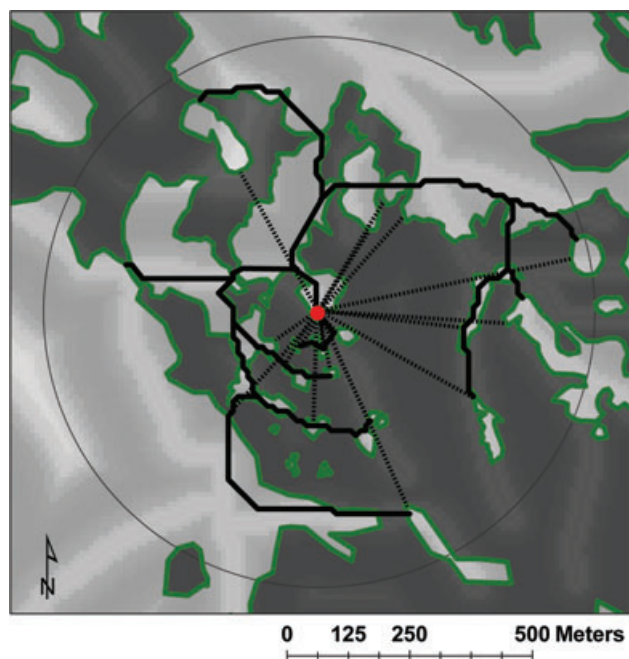
## VIII. MEASURING CONNECTIVITY IN PLANT-POLLINATOR SYSTEMS

Corridors, defined here as structural connections between habitat patches, may often be the exception rather than the rule in fragmented landscapes, so it is important to understand how dispersal connections through the matrix affect pollination dynamics across the landscape (Minor *et al.*, 2009). One commonly adopted technique in landscape ecology for measuring connectivity ( $S_i$ ) involves the use of the incidence function model (IFM) equation:

$$S_i = \sum \exp(-\alpha d_{ij}) A_j^b \quad (1)$$

where  $d_{ij}$  is the distance between a focal patch  $i$  and patches  $j$ ,  $A_j$  is the area of patch  $j$ , with parameter  $\alpha$  scaling the effect of distance on dispersal ( $1/\alpha$  is the average pollinator movement distance), and  $b$  is a parameter scaling the effect of emigration to the area of surrounding patches





**Fig. 7.** An example landscape showing the importance of using functional connectivity (solid lines) *versus* Euclidian distance (dotted lines) to determine connectivity of a focal patch (red central dot) at a spatial scale expected to be important to movements of green hermit hummingbirds (*Phaethornis guy*). Functional connectivity was quantified using actual hummingbird distributions as a response variable in a presence-only species distribution model (MAXENT; Phillips *et al.*, 2006). The movement cost function (dark = high cost, light = low cost) was calculated as the inverse of occurrence probability. A least-cost path algorithm was used to determine the shortest paths. Patches of tropical forest are outlined in green (M.G. Betts & A.S. Hadley, unpublished data). In this case, portions of the landscape with very high functional connectivity tended to be forested riparian corridors.

(Hanski, 1994). The parameter  $\alpha$  has previously been estimated using passive observations of marked animals (Wahlberg *et al.*, 2002a). The second parameter,  $b$ , can also be estimated using mark-recapture data—though performance of IFMs is not tremendously sensitive to this parameter (Prugh, 2009). The IFM thus takes into account the exponential decay typical of dispersing propagules (in this case pollen) as well as hypothesized relationships between the likelihood of pollinator immigration and emigration in relation to the area of surrounding patches. Though a variety of connectivity metrics have been applied in the literature, IFMs are thought to be superior because they contain information about the entire patch network (i.e. the size and distance of neighbouring patches) in relation to species dispersal or movement abilities (Bender, Tischendorf & Fahrig, 2003; Minor *et al.*, 2009; Prugh, 2009).

It is particularly important to consider functional connectivity from the pollinator's perspective as it is not necessarily dependent only on the configuration of plant habitat. Connectivity measured using the Euclidian distance

between patches of plants or flowers may not accurately represent patch connectivity if relative resistance of the intervening landscape elements to pollinator movements varies (Fig. 7; see Section VII.2). A key challenge in adopting a species-centered approach in landscape pollination ecology will be the acquisition of landscape data at sufficient spatial resolution to be relevant to pollinator behaviour (Lonsdorf *et al.*, 2009).

Measuring functional connectivity is notoriously difficult as it necessitates determining the motivation underlying the individual movement (Bélisle, 2005); for instance, lack of movement by a pollinator across an apparent habitat gap could reflect a physical impediment, or simply a lack of motivation (e.g. resources are sufficiently available without necessitating gap crossing). Experimental manipulations to standardize motivation coupled with precise tracking methods are likely to offer the most meaningful assessment of functional connectivity in the field. Techniques relevant to pollinators include translocation, food-titration experiments, giving-up density experiments, and manipulation of nest location. Translocation (Hadley & Betts, 2009) might be particularly useful for territorial pollinators with homing tendencies since the destination and motivation of individuals is controlled; individuals can be moved across specific landscapes differing in composition or configuration and their return path/success monitored. However, the strength of translocation experiments may simultaneously be their weakness; the behaviour of pollinators on translocation does not necessarily correspond to the behaviour of pollinators during daily movements. Studies comparing behaviour on translocation with 'natural' movement behaviour are urgently required. Food-titration experiments (Turcotte & Desrochers, 2003) set up using floral arrays or feeder units in different landscape contexts could be used to assess gap-crossing abilities and perceptual range. Similarly, aspects of marginal value theorem such as 'giving-up density' (GUD) or 'giving-up time' (GUT) experiments can also reveal interesting results relating to foraging decisions under different landscape contexts. Such experiments could examine the number of flowers that remain unvisited in a patch when a forager moves to a new patch, or the amount of time spent at a patch before emigration. Pollination systems appear extremely conducive to these sorts of experiments (e.g. Collevatti, Campos & Schoereder, 1997; Diekotter *et al.*, 2007; Goulson, 2000). Manipulating nesting site location (e.g. placement of hives; see Taki *et al.*, 2010) with respect to known landscape characteristics and food resources may also be useful in determining minimum requirements for persistence.

Because functional connectivity is a species-specific concept (Taylor *et al.*, 1993) for many pollinators it may be more appropriate to measure distance between patches ( $d$ ) in the incidence function model (equation 1) using cost distance modeling (Bunn, Urban & Keitt, 2000) rather than Euclidian distance. This approach has usually relied on experts to estimate the expected 'resistance' values of various types of intervening matrix on a species-specific basis



(e.g. Driezen *et al.*, 2007). A more rigorous approach could be to quantify landscape resistance (i.e. movement costs) *via* functional connectivity experiments as outlined above. Urban *et al.* (2009) argue that using detailed movement trajectories of translocated animals is the most promising method for parameterizing least cost paths—though data to accomplish this are rare. As an initial demonstration of such an approach, we quantified functional connectivity for a traplining hummingbird species using observed movement paths (see Fig. 7 for details).

## IX. SENSITIVITY OF POLLINATION TO HABITAT FRAGMENTATION

Pollination might be relatively insensitive to fragmentation for several reasons. First, as a general rule, effects of habitat fragmentation on biodiversity are often thought to be relatively modest in comparison to habitat loss (Fahrig, 2003). In addition, pollination may be buffered against changes in landscape configuration due to the structure of plant-pollinator networks (Memmott *et al.*, 2004). As noted above, the nested structure typical of plant-pollinator networks means that most specialized plant species are visited by generalist pollinators and *vice versa* (Bascompte *et al.*, 2006). Specialist plants are visited by multiple pollinator species, each of which may display differential sensitivity to landscape characteristics. As landscapes become more fragmented for a pollinator with poor vagility, precluding efficient inter-patch movement for this species, another more vagile species could be expected to adopt the key pollination role. Further, because, by definition, floral-generalist pollinators are capable of using a wider range of floral resources, generalist pollinators are likely to perceive landscapes as having larger amounts of habitat and lower degrees of fragmentation (see Fig. 6A). Specialist plants occurring in isolated patches may therefore still have access to high abundances of generalist pollinators. For these reasons, at the community level at least, there may be robustness in pollination systems to both habitat loss and fragmentation.

However, though the structure of pollination networks has been examined across gradients in such stressors as invasive species (Aizen *et al.*, 2008) and habitat loss (Sabatino, Maceira & Aizen, 2010), to our knowledge, no such study has been completed for landscape fragmentation *per se*. Repeated findings of negative effects of landscape disturbance (habitat loss and fragmentation combined) on pollination success (e.g. Aguilar *et al.*, 2006; Kremen *et al.*, 2004, 2002) suggest that it cannot necessarily be assumed that the nested nature of pollination networks offers effective buffering against all disturbances. Buffering in pollination networks is hypothesized to break down under conditions of extreme cases of habitat loss or fragmentation where densities of many interacting species simultaneously decrease below certain thresholds (see Section X; Fortuna & Bascompte, 2006). Further, if entire functional groups of pollinators respond to fragmentation in similar ways, buffering capacity would be

lost. Finally, fragmentation could potentially affect critical 'hub' species in networks (Olesen *et al.*, 2007); through the loss of a single generalist species multiple links could be removed thwarting much of the network's capacity to buffer. Functionally efficient pollinators may also be those that are most extinction prone contributing to rapid loss of function; indeed, Larsen, Williams & Kremen (2005) demonstrated that habitat loss resulted in preferential loss of such efficient pollinators. For these reasons, we suggest that fragmentation should not be dismissed as a driver of widespread pollination declines until its relative contribution has been quantified.

Despite the fact that there are theoretical reasons for both positive and negative effects of fragmentation, we feel that the potential for negative responses deserves special attention. Unlike Fahrig (2003), who found that effects of habitat fragmentation on biodiversity were as likely to be positive as negative, four of the five existing empirical studies controlling for the effects of habitat amount showed negative effects of habitat fragmentation on pollination. The independent fragmentation effects in pollination systems may not be trivial (Table 2).

As an alternative to the hypothesis that pollination networks will be buffered due to their asymmetrical structure, we suggest some hypotheses for the potential sensitivity of pollination dynamics to fragmentation *per se*. These hypotheses are most likely to apply and be detected in landscapes where distinctions between native habitat and non-habitat are clear (Kremen *et al.*, 2002) and where plant and pollinator habitats are approximately congruent (e.g. forest systems; Aizen & Feinsinger, 1994). First, pollination is multi-faceted (Hegland *et al.*, 2009, but see Memmott *et al.*, 2004), and requires efficient functioning of three major ecosystem components or processes (i.e. plant density, pollinator density, pollinator behaviour) interacting at multiple spatial scales (e.g. plant, patch, landscape). Failure or decline in any of these components or processes is likely to result in reduced or failed pollination, at least at the level of individual plant species. Though changes in plant and pollinator density or pollinator behaviour alone could be sufficient to reduce pollination, there is also potential for initiation of negative feedback loops (Fig. 3). For example, reduced plant fecundity in fragmented landscapes, as an initial result of inefficient pollinator movement (Levey *et al.*, 2005), would eventually result in lower plant density unless inter-patch seed dispersal is biased toward fragmented patches. Low plant densities in fragmented patches should further reduce the benefits to pollinators of visiting these patches (Heinrich & Raven, 1972). We hypothesize that the cumulative interacting effects among the different mechanisms outlined above could contribute to fragmentation sensitivity of pollination systems beyond those observed for individual plant or animal species.

Second, landscape configuration can change animal movement rates and patterns even when there is no measurable effect on density or abundance. For instance, despite higher densities of hermit hummingbirds (*Phaethornis* sp.) in fragmented landscapes (Stouffer & Bierregaard,

1995), landscape fragmentation negatively affects movement (Hadley & Betts, 2009). It is important to consider pollination in terms of a network with variable levels of flow (Dalsgaard *et al.*, 2008). If pollinators avoid crossing non-habitat during their daily movements and alter their movement patterns accordingly (Hadley & Betts, 2009) we would expect to see differences in the volume and pattern of pollen movement in relation to intact landscapes. If matrix inhibits movement, maintaining connectivity among patches may be crucial for inter-patch pollen flow (Fig. 4F). Plant species requiring outcrossing events (i.e. those that are self-incompatible) may be sensitive to even slight reductions in inter-patch movements.

Finally, the requirement for repeated animal movements between flowers and/or patches to obtain sufficient resources for persistence (i.e. landscape supplementation) also makes pollination more vulnerable to the risks posed by fragmentation. Animal dispersal usually only requires a single movement event to a patch during an organism's lifetime to colonize isolated patches and maintain metapopulations (Hanski, 1998); however, if there are insufficient resources within a single patch (Tiebout, 1991), nectar collection requires repeated inter-patch movements by the same individuals. For example, in our tropical montane forest study system, traplining hummingbirds depend on relatively rare, yet high-reward flowers (Stiles & Freeman, 1993), so repeated daily inter-patch movements are necessary, which may result in more chronic risk (Hinsley, 2000). Mortality risk during movements within the matrix can have a substantial impact on metapopulation dynamics even when only a single crossing event is required (Fahrig, 2002). Longer-distance foraging bouts under situations with sparse resources have been shown to reduce pollinator reproductive success (Goodell, 2003).

## X. A NOTE ON LANDSCAPE THRESHOLDS

Previous theoretical (Fahrig, 1998) and empirical work (Andren, 1994; Betts *et al.*, 2007; Radford, Bennett & Cheers, 2005; Tschardt *et al.*, 2008) has demonstrated that the effects of fragmentation are often non-linear. That is, negative effects of fragmentation only occur in landscapes with low amounts of habitat. Though few studies have tested for landscape thresholds in pollination, a study on orchids, *Ptergodium catholicum*, indicated that habitats <385 ha, when separated by urban matrix, were too small to maintain populations of the orchid's sole bee pollinator, *Rediviva peringueyi* (Pauw, 2007). Fragmentation thresholds tend to be relatively low in simulation models (~10% habitat; Fahrig, 1998) and empirical studies (10–30%; Andren, 1994). However, theoretical work has tended to focus on one-time negative consequences of natal dispersal in fragmented landscapes. Therefore, unless mortality in non-habitat matrix is extremely high (Fahrig, 2001; With *et al.*, 1997), most models reveal relatively small effects of fragmentation even at low habitat amounts (Fahrig, 1998).

Because of the possibility for independent effects of fragmentation noted above and the potential for among-taxa interactions, which may drive negative feedback loops, in some systems it might be expected that thresholds in pollination dynamics occur at higher levels of habitat than in the case of individual species' demography. Indeed, a recent simulation study which tested for the independent effects of habitat loss and fragmentation on pollination showed that, owing to such feedbacks, plant-pollinator networks can be disproportionately sensitive to landscape changes; extinction thresholds in pollination networks occurred at 50–60% habitat loss (Keitt, 2009). If limitations to foraging or dispersal due to fragmentation are incorporated, extinctions occurred at even higher habitat amounts (Keitt, 2009). In simulation models, loss of key species within a community is thought to lead to sudden collapse (Kaiser-Bunbury *et al.*, 2010) indicating that rates of decline may not be easily predictable. Despite these points, it is still possible that thresholds could be lower rather than higher, due to the buffering capacity provided by the nestedness of pollination networks (Fortuna & Bascompte, 2006) or if pollinator species are not narrowly tied to the natural habitat type, but capitalize on resources in the matrix.

There are now a variety of statistical tools available to quantify and test statistically for thresholds (Muggeo, 2003; Toms & Lesperance, 2003) so such testing alternative hypotheses regarding the existence and sensitivity of thresholds in pollination systems seems a productive avenue for future research given appropriate empirical data; to our knowledge no threshold models have yet been applied in pollination studies. Finally, future simulation models should consider the cumulative effects posed by the regular gap-crossing behaviour of species requiring multiple resource patches to satisfy their life-history requirements (*sensu* Dunning *et al.*, 1992).

## XI. IMPLICATIONS FOR FUTURE RESEARCH AND CONSERVATION PLANNING

Given the high degree of uncertainty about the effects of fragmentation on pollination systems beyond those attributable simply to habitat loss (Fig. 3), it will be particularly important to consider configuration in future landscape pollination ecology studies. The fact that, in nature, the processes of habitat loss and fragmentation often occur together and are correlated does not imply that there is no scientific or conservation need to disentangle them. Without understanding the drivers of pollination and pollinator declines it will be impossible to conceptualize optimal landscape designs for maintaining or enhancing pollination services (Brosi *et al.*, 2008; Lonsdorf *et al.*, 2009; e.g. Fig. 1). Though the existing body of literature has done much to elucidate the importance of landscape structure as a whole on pollination dynamics, failure to effectively separate the independent effects of composition and configuration has hampered the potential to identify

causes of the revealed patterns. We expect that variation across studies in the effects of ‘fragmentation’ owes much to artifacts of the sampling regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss and (2) mis-matches in spatial scale between landscapes studied and the ecological processes of interest. Here, we provide three recommendations to facilitate research in the field of landscape pollination ecology.

First, more emphasis should be placed on designing studies that disentangle the different aspects of pollination in disturbed landscapes. Landscape disturbance clearly has negative impacts on pollination in most systems (Aguilar *et al.*, 2006). These effects may be partly due to changes in the plant community (Honnay *et al.*, 2005) or to changes in the pollinator community and behaviour (Steffan-Dewenter & Westphal, 2008). Controlled, replicated experiments such as conducted by Tewksbury *et al.* (2002) and Townsend & Levey (2005) on movement corridors are ideal, but may become intractable if the objective is to consider the complexities of connectivity associated with different sorts of matrix. Since large-scale landscape manipulations are challenging and expensive, mensurative experiments designed explicitly to disentangle the role of various landscape elements may be the most effective (Betts *et al.*, 2006). In cases where data have already been collected or correlated variables are unavoidable, attempts should still be made to disentangle effects statistically (Smith *et al.*, 2009).

Second, despite the multitude of ways that pollinator movement ability and movement decisions affect pollination services, we still know very little about even basic movement patterns of pollinators (Ghazoul, 2005). Thus, the ‘pollinator movement’ hypothesis—that observed effects of landscape disturbance are due to restrictions in movement rather than plant or pollinator density—still remains largely untested. Testing this hypothesis will require the integration of pollination, landscape and behavioural ecology. Future work could be a combination of experimental and observational studies, designed to understand better the movement capacities and behavioural decisions of pollen vectors in relation to the spatial distribution of resources. Critical information will be required on animal dispersal distances, daily movement distances, gap-crossing capacities, movements in relation to edges, energy requirements and optimal foraging decisions. Recent technological improvements including reductions in the size of radio transmitters (Wikelski *et al.*, 2006), harmonic radar (Osborne *et al.*, 1999; Riley *et al.*, 2005) and radio-frequency identification devices (Ohashi, D’Souza & Thomson, 2010) provide the opportunity to observe movement behaviour of pollinators across unprecedentedly large gradients in spatial and temporal grain and extent. Studies should be designed to examine landscape resistance and determine functional connectivity for pollinators and therefore associated plants (Bélisle, 2005; Hadley & Betts, 2009).

Finally, further progress in this field will require consistency in terminology and clear methodologies. We stress the recommendations of Fahrig (2003) and

Lindenmayer & Fisher (2007) that the term ‘fragmentation’ should be reserved for the independent effects of landscape configuration while the term ‘habitat loss’ should reflect changes in landscape composition. If a study is not able to separate composition from configuration, using the terms ‘landscape disturbance’ or ‘landscape-level effects’ would avoid inaccurately assigning a result to either process and further propagation of the confusion that arises from using the same term to describe critically different processes. Studies should clearly state and describe (1) the response variables of interest, (2) the spatial scale(s) of examination, (3) landscape-scale predictor variables and whether or not these represent landscape composition or configuration. Reporting the effect sizes of composition and configuration variables from multivariate statistical models (*sensu* Smith *et al.*, 2009) is essential for interpretation of results, and will be essential for future meta-analysis on this topic. We hope that following these general guidelines will help direct crucial future work on the effects of habitat fragmentation on pollination.

## XII. CONCLUSIONS

(1) Landscape-scale disturbance results in two often inter-related processes: (1) habitat loss, (2) disruptions of habitat configuration (i.e. fragmentation). Understanding the relative effects of such processes is critical in designing effective management strategies to limit pollination and pollinator decline.

(2) We reviewed existing work and found only six of 303 studies considering the influence of landscape context on pollination separated the effects of habitat loss from fragmentation (Fig. 2). Therefore, almost no research exists on whether landscape composition (i.e. the relative abundance of land cover types, particularly the amount of habitat) or landscape fragmentation (e.g. corridors, patch size and shape), or both, are most critical to pollination dynamics (Table 2).

(3) Landscape disturbance primarily influences three components of pollination interactions: pollinator density, pollinator movement, and plant demography (Fig. 3). We argue that effects of habitat loss on each of these components are likely to differ substantially from the effects of fragmentation, which is likely to be more complex and may influence each pollination component in contrasting ways.

(4) Given the high degree of uncertainty about the extent to which fragmentation affects pollination systems, we argue that it is particularly important to consider configuration in future landscape pollination ecology studies. Without understanding the drivers of pollination and pollinator declines it will be impossible to conceptualize optimal landscape designs for maintaining or enhancing pollination services (Fig. 1).

(5) We expect that variation across studies in the effects of ‘fragmentation’ owes much to artifacts of the sampling



regimes adopted, particularly (1) incorrectly separating fragmentation from habitat loss and (2) mis-matches in spatial scale between landscapes studied and the ecological processes of interest. We suggest that researchers adopt an organism-based view of the landscape and measure elements of interest accordingly.

(6) We provide three main recommendations for future studies. (1) Studies designed to disentangle the independent effects of habitat loss and fragmentation are essential for gaining insight into landscape-mediated pollination declines, implementing effective conservation measures, and optimizing ecosystem services in complex landscapes. (2) We recommend a combination of experimental and observational studies, designed to understand better the movement capacities and behavioural decisions of pollen vectors. (3) Further progress in this field will require consistency in terminology and clearly defined methodologies.

### XIII. ACKNOWLEDGMENTS

We thank W.D. Robinson and S. Frey for useful discussion. This manuscript was improved by comments from two anonymous reviewers. This research was funded by a National Science and Engineering Council of Canada (NSERC) PGS-D to A.S.H. and a National Science Foundation (NSF) grant DEB-1050954 to M.G.B.

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## XV. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Appendix S1.** Details of the 303 articles examined.

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(Received 7 October 2010; revised 23 September 2011; accepted 30 September 2011; published online 17 November 2011)