REVIEW AND SYNTHESIS

Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change

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Abstract

Many ecosystem services are delivered by organisms that depend on habitats that are segregated spatially or temporally from the location where services are provided. Management of mobile organisms contributing to ecosystem services requires consideration not only of the local scale where services are delivered, but also the distribution of resources at the landscape scale, and the foraging ranges and dispersal movements of the mobile agents. We develop a conceptual model for exploring how one such *mobile-agent-based ecosystem service* (MABES), pollination, is affected by land-use change, and then generalize the model to other MABES. The model includes interactions and feedbacks among policies affecting land use, market forces and the biology of the organisms involved. Animal-mediated pollination contributes to the production of goods of value to humans such as crops; it also bolsters reproduction of wild plants on which other services or service-providing organisms depend. About one-third of crop production depends on animal pollinators, while 60–90% of plant species require an animal pollinator. The sensitivity of mobile organisms to ecological factors that operate across spatial scales makes the services provided by a given community of mobile agents highly contextual. Services vary, depending on the spatial and temporal distribution of resources surrounding the site, and on biotic interactions occurring locally, such as competition among pollinators for resources, and among plants for pollinators. The value of the resulting goods or services may feed back via market-based forces to influence land-use policies, which in turn influence land management practices that alter local habitat conditions and landscape structure. Developing conceptual

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models for MABES aids in identifying knowledge gaps, determining research priorities, and targeting interventions that can be applied in an adaptive management context.

INTRODUCTION

Ecosystem services are functions provided by nature that improve and sustain human wellbeing (Daily 1997). Some ecosystem services, such as pollination, pest control and seed dispersal, are produced at a local scale by mobile organisms foraging within or between habitats (Gilbert 1980; Lundberg & Moberg 2003; Sekercioglu 2006). We call these services mobile agent-based ecosystem services (MABES). Although these mobile organisms deliver services locally, their individual behaviour, population biology and community dynamics are often affected by the spatial distribution of resources at a larger, landscape scale. Managing for mobile organisms and the services they provide therefore requires considering not only the local scale where services are delivered, but also a landscape scale that reflects both the spatial distribution of resources and the foraging and dispersal movements of the organisms themselves. MABES have both direct (immediate) and indirect (via other ecosystem services) values, corresponding respectively, to their regulating and supporting roles (Millennium Ecosystem Assessment 2005). For example, the direct (regulating) value of pollination services to humans is the marginal increase in production of market-based or subsistence crops, fibre, forage, timber and non-timber forest products (e.g. firewood, medicinal products and wild fruits) resulting from animal pollination. The indirect (supporting) value is the marginal increase, due to animal pollination, in reproduction of wild plants that play a role in other ecosystem services.

Here we develop a conceptual model of how pollination services, a MABES that is comparatively well understood, respond to land-use change. We synthesize the literature to determine response of each component of the model to land-use change, and identify important gaps in our knowledge. Second, as a case study, we apply this conceptual framework to managing agricultural lands for improved pollination services. Third, we generalize the model to other MABES, such as pest and disease control. Services not covered by this MABES conceptual framework are those produced by sessile organisms (e.g. vegetation-based services such as water filtration, flood and erosion control)

and/or those that occur at a global scale (e.g. carbon storage and sequestration).

CONCEPTUAL MODEL FOR POLLINATION SERVICES

Pollination services are provided both by wild, free-living organisms (chiefly bees, but also many butterflies, moths, flies, beetles and wasps, and selected other invertebrates, birds and mammals), and by commercially managed bee species (primarily the honey bee, *Apis mellifera*). We focus on bees, the predominant and most economically important group of pollinators in most geographical regions. Pollinators are important in 35% of global crop production (Klein *et al.* 2007). Sixty to eighty per cent of wild plant species require animal pollinators, while a much larger number may benefit from animal visitation (Husband & Schemske 1996; Kearns *et al.* 1998; Ashman *et al.* 2004). Concerns about the loss of pollinators and the services they provide have grown over the last decades (Allen-Wardell *et al.* 1998; Kearns *et al.* 1998), but relatively little information exists on the status of pollinators or of pollination function. These concerns are warranted, based on recent evidence of declines at local or regional scales (e.g. Larsen *et al.* 2005; Biesmeijer *et al.* 2006), evidence for elevated extinction rates across all taxa (Dunn 2005; Millennium Ecosystem Assessment 2005) and the precautionary principle. In addition, declines in abundance of the most important commercially managed crop pollinator (*Apis mellifera*) are well documented in the USA (National Research Council of the National Academies 2006) and elsewhere (e.g. Griffiths 1986). These declines are due chiefly to the establishment of a disease-carrying mite, *Varroa destructor*, and have led to pollination shortages and price increases for pollination rental fees for selected crops (e.g. almond, Sumner & Boriss 2006).

In our conceptual model, alterations in pollinator communities are closely linked to changing land-use practices (Fig. 1). We first describe the model briefly, and then review what is known about the response of each component and linkage. At the site scale (Box A in Fig. 1), land-use and management practices affect local community composition of plants, their pollinators, and the biotic and
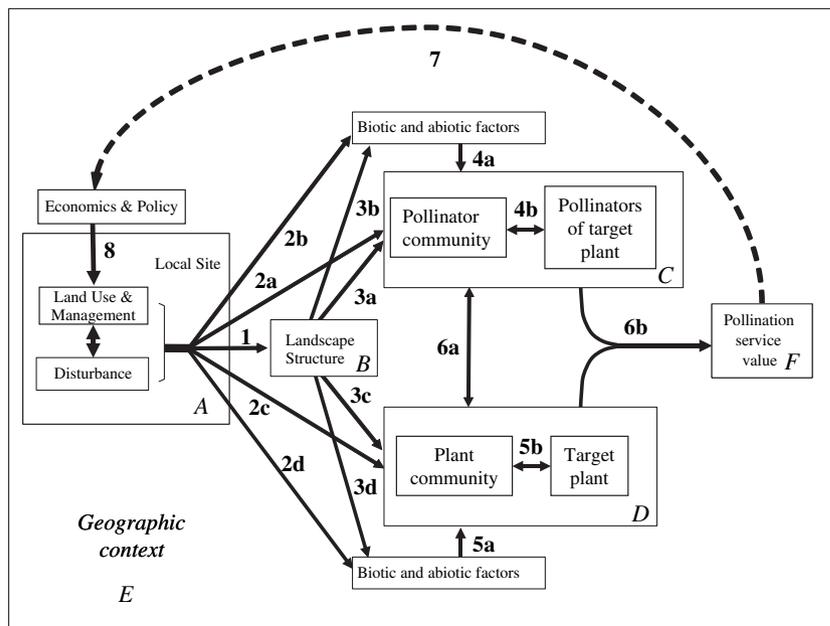
Figure 1 Conceptual framework for impacts of land-use change on pollination services, incorporating market-based forces and policies, in addition to the biology of the organisms involved. Letters refer to boxes; numbers refer to arrows; see text.

abiotic factors affecting both groups (2A–D). Site scale effects aggregate to create landscape structure (BOX B, 1), that is, the spatial configuration of different types of natural, seminatural and anthropogenic habitats, which in turn influences all of these communities (3A–D). For example, landscape structure influences the temporal and spatial availability of food, nesting, overwintering and mating sites for pollinators.

Any animal-pollinated plant (hereafter referred to as 'target plant', which can be crop or wild) is visited and pollinated by only a subset of species from the entire pollinator community. The abundances of pollinators in the wild are influenced by abiotic and biotic factors, including predators, pathogens, parasites and competitors (4A,B); and by the availability of critical resources (2A, 3A AND 6A). The abundance of the target plant is similarly influenced by its own mutualists (6B), predators, pathogens, competitors and abiotic factors (5A,B); and by resource and habitat distribution (2C AND 3C). The interaction between the target plant and its pollinators (6B) leads to the pollination service value (BOX F). This interaction is highly contextual, depending upon the composition of both plant and pollinator communities surrounding the target plant (BOXES C AND D) and their interactions (6A). The value of the pollination services provided depends on the geographical context in which it occurs (BOX E), including ecological, economic, social and political factors. This value in turn may feedback to influence the economic or policy environment (7), which affects decisions about land-use and management practices (8), influencing levels and types of disturbance at site and landscape scales (BOXES A, B, 1).

Commercially managed pollinators also fit within this conceptual model: they are influenced directly and indirectly by the same site and landscape-level processes as other pollinators (e.g. availability of pollen and nectar, Pyke *et al.* 1977; Steffan-Dewenter & Kuhn 2003). In turn, these managed pollinator species influence the pollinator and plant communities through competitive and mutualistic mechanisms. Notably, however, the distributions and abundances of commercial pollinators are also, and in some cases, primarily, driven by economic forces (e.g. USA, Muth *et al.* 2003), such as the market demand for pollination services by growers, and the price of hive products (e.g. honey, pollen and wax).

LAND-USE CHANGE: EFFECTS ON POLLINATORS AND PLANT–POLLINATOR INTERACTIONS

Human impacts have modified the landscape through fragmentation, degradation and destruction of natural habitats and the creation of new anthropogenic habitats. Estimates of complete habitat conversion vary by biome from 0.4% (tundra) to 48.5% (tropical/subtropical dry broadleaf forests), but a much larger area is directly influenced by human activities to some degree (Sanderson *et al.* 2002; Hoekstra *et al.* 2005). Changes in land-use and landscape structure influence pollinators, target plants and their interactions at individual, population and community scales.

Pollinators (Box C)

The response of bee individuals, populations and communities to land-use change is largely driven by the spatial and temporal distribution of floral, nesting and over-wintering

resources (2C AND 3C) in relation to foraging and dispersal capabilities of bees. These components may occupy the same locality or may be dispersed across the landscape, producing a patchwork of partial habitats (*sensu* Westrich 1996). Floral resources (BOX D, pollen, nectar, oils and resins) are an important determinant structuring pollinator communities (6A). Bee abundance and species richness (BOX C) is positively associated with the abundance and richness of flowering plant species (BOX D) (Banaszak 1996; Steffan-Dewenter & Tscharntke 2001; Potts *et al.* 2003a). More specifically, studies have found that the species richness of bees is affected by the diversity of nectar sources, the ratio of pollen to nectar energy content, and floral morphology (Bosch *et al.* 1997; Potts *et al.* 2003a). Greater floral diversity creates a wider array of foraging niches for different functional groups of visitors (Fenster *et al.* 2004). Environmental changes that alter the spatial and temporal distribution of floral resources influence pollinator community composition: for example, in a 50 year chrono-sequence of Mediterranean pine–shrub community regenerating following fire, bee community composition closely tracked floral composition and rewards (Potts *et al.* 2003b).

Nesting sites are also important determinants of pollinator community composition. Bees exhibit a variety of nesting habits, including tunnelling in bare ground, using pre-existing cavities (e.g. pithy stems, small rock cavities or abandoned insect burrows), excavating dead wood, and constructing nests inside larger cavities in or on trees, rocks or rodent nests (e.g. social nesters like *Apis*, *Bombus* and stingless bees). The diversity and specificity of nesting habits among pollinating species means that the quantity and quality of nesting resources greatly influence bee community composition at any given point. Potts *et al.* (2005) showed that the composition of a diverse bee community in Israel was partially determined by the local presence of bare ground, potential nesting cavities, steeply sloping ground, plants with pithy stems and pre-existing holes. Similarly, the density of stingless bee nests was positively associated with the local abundance, size and species of nest trees in tropical forests (Eltz *et al.* 2002; Samejima *et al.* 2004). Compared with floral resource use, however, much less is known about nesting requirements of most bees. Further studies are needed to document nesting site and substrate requirements for individual species, to determine whether nest sites are limiting resources, and to understand how other factors within a bee's foraging range, such as floral resource distribution, may affect nest site selection.

Land-use change alters the distribution of both floral and nesting resources (Tscharntke *et al.* 2005), affecting individual behaviour, population dynamics and community composition of bees. Central place foraging from a fixed nest site anchors individual foraging movements relative to

resources that vary in space and time, and likely increases sensitivity to changes in habitat/landscape that reduce the continuity of resources. Sensitivity to changes in continuity of resources will depend on species-specific flight capacity, which is positively correlated with bee body size (Gathmann & Tscharntke 2002). Although larger bees can access resources further from their nests, such bees also have higher resource demands (Cresswell *et al.* 2000), which could exclude larger species from areas with limited resources, as has been observed in some systems (e.g. intensive agricultural areas, Larsen *et al.* 2005).

Individual pollinators alter their foraging behaviour in response to changes in landscape structure. Examples include following corridors of vegetation to reach nectar or pollen sources (Haddad *et al.* 2003); avoiding edges created by roads or habitat boundaries (Rasmussen & Brodsgaard 1992; Ricketts 2001; but see, Kreyer *et al.* 2004), increasing foraging times in patches in simple landscapes with few alternative flower resources, or switching to locally available, non-preferred species if preferred plant hosts are too distant (Pyke *et al.* 1977; Steffan-Dewenter *et al.* 2001; Williams & Kremen in press). The quality of the matrix surrounding the remnants of the original habitat will have a strong influence on individual pollinator movements. For example, a sufficiently large matrix that is devoid of flowers may act as a barrier for pollinator movement, while one occupied by a mass-flowering crop can promote connectivity and provide nectar and pollen resources during periods of floral scarcity in the habitat remnants (Westphal *et al.* 2003; but see Chacoff & Aizen 2006).

At the population level, three genetic and demographic characteristics may predispose bee populations to be particularly vulnerable to habitat and landscape changes that reduce population size. First, bees are haplodiploid, which reduces the effective population size (N_e) to at most 3/4 that of equivalently sized diploid populations with approximately even sex ratios. Second, single-locus sex determination contributes to reduced N_e, because homozygotes at the sex locus become sterile diploid males. This occurs more frequently in small or inbred populations (Cook & Crozier 1995). Third, reproductive rates of solitary bees are often surprisingly low (Minckley *et al.* 1994). These three factors exacerbate the well-known extinction risks facing small populations through genetic or demographic stochasticity (Zayed & Packer 2005). The role of diploid male production in contributing to extinction risk in small populations of bees deserves additional empirical investigation.

The loss and fragmentation of natural habitat could reduce gene flow and re-colonization rates among fragments, leading to lowered persistence not only of subpopulations but also of meta-population networks (Hanski 1998; Zayed *et al.* 2005). This view of habitat

fragmentation perceives surrounding matrix as devoid of resources, and inimical to survival. Empirical studies of bee populations and communities, however, reveal a range of responses to fragment size, including positive, negative and neutral (Becker *et al.* 1991; Aizen & Feinsinger 1994; Donaldson *et al.* 2002; Tonhasca *et al.* 2002). This variability in response to fragmentation is likely due to differences in dispersal ability and habitat and floral specificity among pollinator species (Saville *et al.* 1997; Law & Lean 1999; Steffan-Dewenter 2003; Zayed *et al.* 2005). Many pollinator species use floral or nesting resources associated with the surrounding matrix habitat (Eltz *et al.* 2002; Cane *et al.* 2006; Winfree *et al.* 2006; Kim *et al.* in press; Williams & Kremen in press), and thus do not fit the classic island biogeography model of strict dependence on a natural habitat patch. Our knowledge of dispersal and population structure in bees is extremely limited (Estoup *et al.* 1996; Danforth *et al.* 2003; Zayed *et al.* 2005), and is a critical area for further research. In addition, determining the carrying capacity of different habitats or habitat mosaics for bee populations is essential for understanding how to manage bee populations and pollination services.

At the community level, pollinator richness may initially increase in response to disturbances that are intermediate in intensity and/or frequency (e.g. Vulliamy *et al.* 2006), but become depauperate and relatively homogeneous under intense disturbance (e.g. Chacoff & Aizen 2006) or in 'climax' habitats consisting of relatively few plant species (e.g. Winfree *et al.* 2006). Pollinator species likely to benefit from a moderate level of disturbance include those that use resources that occur in human-dominated matrices like agricultural or urban/suburban areas (Westrich 1996; Westphal *et al.* 2003; Cane *et al.* 2006; Winfree *et al.* 2006), and ground-nesting bees that require patchy vegetation characteristic of early successional stages. Along land-use change gradients, reduced diversity is often associated with decreased overall bee abundance at the community level (Steffan-Dewenter & Tscharntke 1999; Klein *et al.* 2002, 2003; Steffan-Dewenter *et al.* 2002; Ricketts 2004; Larsen *et al.* 2005; Chacoff & Aizen 2006), suggesting that under anthropogenic disturbance, little or no density compensation takes place (Kremen & Chaplin-Kramer in press).

Almost no data exist on how pollinator communities disassemble and what the resulting consequences are for pollination function. Plant–pollinator networks are reciprocally redundant (Memmott *et al.* 2004), so that few plant species are likely to lose all their pollinator species as pollinator communities disassemble. Studies offer alternative predictions of how rapidly pollination function would be affected if pollinator communities disassembled non-randomly with respect to number of linkages (Memmott *et al.* 2004) or pollinator effectiveness (Morris 2003), but only one empirical example of community disassembly and

its effect on pollination function exists (Larsen *et al.* 2005). This study found that larger, more effective pollinators were also more sensitive to land-use change, leading to rapid loss of function relative to random (linear) loss. Additional studies that simultaneously examine disassembly of pollinator communities and characterize pollinator effectiveness are needed to test the predictions of Morris (2003) and Memmott *et al.* (2004).

Predators, parasitoids and parasites of bee species (4A) also respond to land-use change at individual, population and community levels (2B AND 3B). Natural enemies of pollinators may alter searching behaviour and attack rate of hosts in response to altered landscape structure or host density, as occur, for example, in crop monocultures or commercially managed bee colonies (Kareiva 1985; With *et al.* 2002; Cronin 2003). Predators and parasitoids of bee species declined in species richness and caused less mortality for bees in isolation from natural habitat in several systems (Tscharntke *et al.* 1998; Klein *et al.* 2006), but changes in food web structure can also increase parasitism of solitary bees in highly modified landscapes (Tylianakis *et al.* in press). Little is known about the relative importance of top-down (predators, parasitoids and parasites, 4A) vs. bottom-up (floral and nesting resources, 6A) forces in determining bee population responses to land-use change.

Abiotic factors like pesticides (4A) are an additional aspect of land use that can increase mortality rates (Johansen 1977) or alter foraging behaviour (Morandin *et al.* 2005). Often, the intensity of pesticide use is correlated with decline in availability of floral and nesting resources (Kremen *et al.* 2002; Tscharntke *et al.* 2005), and disentangling the relative effects of each is an important challenge.

Pollination of the target plant (6b)

The vulnerability of plant reproduction to land-use change depends on the degree to which a species relies on external pollinators and how sensitive pollination processes are to landscape change. Pollination of a target plant can be affected by change at the spatial and temporal scales of the flower, the individual, and the population. These effects are modulated both by plant (BOX D) and pollinator (BOX C) community composition, which also respond to land-use change (2A,C, AND 3A,C).

Species-specific plant characters, including breeding system, specialization, and floral traits, strongly influence the vulnerability of a plant species to pollination deficits that may arise from landscape change. The breeding system determines a plant's overall dependence on pollinators for sexual reproduction (Barrett & Harder 1996). Plants that primarily self-pollinate will be largely unaffected by changes in pollinator abundances and identity, but reproduction of obligate outbreeders can be altered dramatically by changes

in the pollinator community. In addition, although self-compatible plants do not require outcross pollen for fertilization, they often produce more seeds and/or larger fruits (e.g.Greenleaf & Kremen 2006a), more vigorous offspring (Marshall 1991) and/or show greater recruitment into the next generation (Herrera 2000) when cross-pollinated.

The level of specialization between a plant and its pollinators further determines the likelihood of disruption of the plant–pollinator interaction (Bond 1995; Aizen *et al.* 2002; Vázquez & Simberloff 2002), and thus its sensitivity to land-use change. In principle, the pollination of a generalist plant is buffered against the loss of any particular pollinator, whereas such loss may mean reproductive failure in a highly specialized plant species. A specialist plant, however, has a reduced risk of losing service if its pollinator is a generalist which is itself buffered against extinction (Vázquez & Simberloff 2002; Ashman *et al.* 2004). Such asymmetries between plant and pollinator specialization indeed appear to be the norm (Vázquez & Aizen 2004). Despite the redundancy and asymmetry common to plant–pollinator networks (Memmott *et al.* 2004), a plant could still be at risk of pollinator failure if it relies on a guild of pollinators whose members respond similarly to a given anthropogenic effect (Corbet 2000). Declines of bumble bees in Europe, especially long-tongued species, provide a worrisome example (Goulson *et al.* 2005). An important area for both theoretical and empirical works is to characterize pollinators in plant–pollinator webs by functional traits (e.g. tongue length, body size, foraging distance, nesting habit, flight temperature threshold and/or daily and seasonal flight window), and response to disturbance (e.g. Larsen *et al.* 2005), and then predict the effects of loss of different functional groups on plant pollination.

Plants may alter the number and size of flowers or the amounts and qualities of pollen and nectar produced, when local disturbance (e.g. land-use change and crop management practices) influences the amount of light, water and nutrients received (reviewed in Aizen & Vázquez 2006). Thus, disturbance potentially influences plant attractiveness and rewards for pollinators (Brody & Mitchell 1997; Goulson *et al.* 1998). Changes in plant attractiveness can alter the behaviour of pollinators, which affects pollen transfer and reproductive success (Pyke *et al.* 1977; Pleasants 1981; Barrett & Harder 1996). Nonetheless, over the compressed time scale of human-induced landscape change, the individual traits of plant species (e.g. breeding system, specialization and floral traits) are largely static factors (but see Washitani *et al.* 1994) that operate principally by affecting the sensitivity of a target plant species to habitat and landscape change.

Patch and population-level attributes such as floral density, patch size and patch isolation also influence the interactions of the target plant with pollinators (Kunin 1997; Ghazoul 2005). Unlike individual traits, these population attributes are likely to be affected directly and rapidly by changes in landscape structure resulting from human disturbance or management practices (2C AND 3C). These patch characteristics affect rates of visitation to the patch and within-patch behaviour of pollinators, thus influencing the quantity and quality of pollen that reaches the stigma. For example, the amount and proportion of conspecific pollen, the number of pollen donors and/or the proportion of outcrossed pollen deposited all influence fruit and seed set (Waser & Price 1983; Snow 1990; Harder & Barrett 1996). Small or isolated populations may suffer decreased reproduction due to lowered quantity and/or quality of pollen relative to non-isolated populations (Jennersten 1988; Donaldson *et al.* 2002). Such effects can result from lower visitation rates by pollinators (Groom 1998; Duncan *et al.* 2004) or to a lack of compatible donor plants (Cunningham 2000; Wolf & Harrison 2001). Although some studies show that even highly isolated plants still receive sufficient outcrossed pollen (Nason & Hamrick 1997; White *et al.* 2002), a recent meta-analysis found a significantly negative effect of habitat fragmentation on pollination of both self-incompatible and self-compatible plants, and a strong correlation of this effect with reproductive success. Self-incompatible plants, however, are much more likely to suffer reduced reproduction due to fragmentation (Aguilar *et al.* 2006).

Delivery of pollination services to the target plant also depends on the community of plants around the target plant (BOX D, 5B). The plant community directly affects pollinator availability by either decreasing the frequency of pollinator visits to the target plant through competition (Pleasants 1981), or increasing it via facilitation (Waser & Real 1979; Moeller 2004). When floral resources are limited, plant species that offer relatively high rewards should outcompete less rewarding plant species (see Cartar 2004) and receive more frequent and consistent visitation by generalist pollinators. These effects may be transient if resources are non-renewing, but lead to higher visitation rates and potential fitness advantages for more rewarding plants that also exhibit faster renewal of rewards (Dreisig 1995). In communities with multiple plant species competing for pollinators, interspecific pollen transfer can also dramatically reduce effective pollination (Waser 1978; Campbell & Motten 1985). In contrast, abundant and diverse floral resources may facilitate visitation to the target plant when the target plant is relatively rare (Moeller 2004), or to the entire community, although data are lacking. Thus, modifications of the surrounding vegetation may strongly affect pollination function to the target plant either negatively or positively by altering both pollinator availability and

effectiveness in delivering conspecific, outcrossed pollen. Many of the effects of plant community on pollination service may operate at spatial and temporal scales larger than the immediate vicinity of target individual(s). A reasonable, although little studied, hypothesis is that plant communities whose flowering brackets the target plant may increase pollination to the target plant and/or the community and stabilize pollination service within and between seasons (Waser & Real 1979; Handel 1997), a subject with important applications for pollination management of both endangered plants and crops.

Finally, the quantity and quality of pollen received by a target plant also depends on the community composition of pollinators (Box C). Pollinator taxa vary in their effectiveness as pollinators (Herrera 1988; Pellmyr & Thompson 1996) due both to species-specific differences in foraging behaviour and morphology, and to interactions between pollinating species (4B). Pollinator taxa vary in their constancy to the target species within a foraging bout, and thus in the proportion of conspecific pollen delivered (Campbell & Motten 1985). The patterns of pollinator movement within- and between-individual plants of the target species further determines the amount of self- vs. outcrossed pollen deposited (Harder & Barrett 1996) and the number of pollen donors (Snow 1990). Interspecific differences in pollinator morphology and interactions with the floral parts also affect the quantity and quality of pollen delivered (Harder & Barrett 1996; Castellanos et al. 2003). Pollinator species differ not only in how much high-quality pollen they deposit, but also in how much pollen they remove from the system. The value of a given species as a pollinator depends on the deposition to removal ratios relative to other pollinators that are present, and the extent that pollen is limiting (Thomson & Thomson 1992). Thus a pollinator species that deposits much pollen but also removes much can be a 'good' pollinator (if no other pollinators that remove less pollen co-occur) or a 'bad' pollinator (if co-occurring pollinators deposit equal or greater amounts of pollen but remove less). Different species may also enhance each others effectiveness as pollinators through behavioural interactions (e.g. Greenleaf & Kremen 2006b), or act in a complementary fashion that improves pollination, as for example, by delivering pollen to different stigmas or parts of the same stigma, and thus fertilizing a greater number of ovules within a flower (Chagnon et al. 1993). Relatively little is known about interspecific facilitation and complementarity in improving pollination success.

THE VALUE OF POLLINATION SERVICES (BOX F)

Pollination services are valuable, both for direct production of human-utilized plant products, and for reproduction of plants that contribute to other ecosystem services. Nonetheless, many important staple food crops do not require animals for pollen transfer, suggesting that food quantities might be little altered under pollinator shortages. Only 35% of global plant-based crop production benefits from animal pollinators to some degree; this includes 107 fruit and vegetable crops of which 10% are obligately dependent on animal pollinators, 75% have improved production due to animal pollinators, 8.5% do not benefit, and 6.5% are unknown (Klein et al. 2007). Although the larger component of food production is pollinator-independent, important components of food production, food diversity, food security, food price stability and human nutrition rely strongly on animal pollinators (Steffan-Dewenter et al. 2005). For example, animal-pollinated foods supply a large proportion of essential micronutrients such as vitamin C (National Research Council of the National Academies 2006). Further work is needed to quantify the role of pollinators in stabilizing the human food supply and contributing to human health and wellbeing. In particular, how do experimental results showing positive effects of animal-mediated pollination at the plant level translate into yield and economic benefit at the field level, for different crops and landscape contexts?

Economic calculations of the value of pollination services (commercial plus wild) vary widely but range from $112 to 200 billion annually at the global scale (Costanza et al. 1997; Kearns et al. 1998). Estimates vary in large measure because different underlying approaches were used for establishing values. For example, Muth & Thurman (1995) state that the value of commercial pollination services is the amount farmers pay to beekeepers to rent bees, and critique other studies (e.g. Robinson et al. 1989a) for inflated estimates of pollination service values. Services from wild bees could similarly be estimated as the amount that would need to be paid to replace wild bees by honey bees. These lower-bound estimates of the value of pollination services '*from the farmer's perspective*' do not capture the much higher value to consumers. The value to consumers is measured as the 'consumer surplus': how much more consumers would have to pay for pollinated food products if pollination services became scarce, thereby reducing supply (e.g. Southwick & Southwick 1992). This value, calculated at the margin, is dwarfed by yet another assessment. Here, value is measured as the proportion of the total value of the crop that depends on pollinators, and can be decomposed into the contributions from wild (Losey & Vaughan 2006) and commercial (e.g. Robinson et al. 1989a) pollinators. This estimate represents the *current* contribution that pollinators make to gross production; the component contributed by wild pollinators represents the current subsidy that nature is providing. Such estimates are near the upper bound of the pollination service value, as *future* adaptive responses by

farmers and consumers to pollinator scarcity are not being considered (Southwick & Southwick 1992; Muth & Thurman 1995). These responses, such as adopting alternative crops or techniques that reduce farmer's dependence on pollinators, would lower the value of pollination services, as would consideration of net rather than gross revenues (Olschewski *et al.* 2006). Future studies should estimate and report both lower and upper bound measures.

Several local-scale studies have determined the relationship between landscape structure and the value of pollination services provided by wild bees (upper bound). The value of pollination services may be estimated by measuring change in seed or fruit set of open-pollinated flowers exposed to natural levels of pollinators against exclusion treatments in which only self or wind pollination occurs (e.g. Blanche & Cunningham 2005; Morandin & Winston 2005). In Costa Rica, the enhanced value of coffee production attributed to wild bee pollinators living in nearby forests was estimated as $393 ha^{-1} of forest (Ricketts *et al.* 2004), an order of magnitude above that estimated in Indonesia (Priess *et al.* in press). The difference was due in part to the much higher proportion of forest area in the Indonesian study, and illustrates how lack of knowledge of the relationship between bee population abundance and natural habitat area can affect such economic valuations (see also Kremen 2005). In canola in northern Canada, Morandin & Winston (2006) found that flowers in fields near uncultivated areas produce greater seed yields due to greater pollination services from a more diverse and abundant wild bee community. Extrapolating to the field scale, they suggest that farmers could maximize profits by retiring up to 30% of the field area from production, so as to receive higher yields on the remaining 70%. More studies like the Morandin & Winston (2006) study are needed that explicitly predict the economic tradeoffs between alternative land management schemes. To best inform land managers, future studies should strive not only to predict but also empirically evaluate the effects of alternative management practices on pollinator communities, pollination services, crop yields (plant and field level) and net revenues. Integrated studies that measure not only pollination but also the effects of other agricultural inputs (water, nutrients and pest control) are needed to determine precisely the yield effects of animal pollination.

Among wild flowering plants, 60–90% of all flowering plant species require an animal pollinator for reproduction, depending on the biome (Axelrod 1960; Bawa 1990). In nature, many wild plant populations are 'pollen-limited', meaning that untreated individuals set fewer fruits or seeds than experimental plants supplemented with cross-pollen (62–73% of cases reviewed, Burd 1994; Ashman *et al.* 2004). The extent to which pollen limitation affects not only reproduction, but also the fitness (e.g. Kolb 2005) and population dynamics of plants is little studied.

Like crops, wild plant species may respond to animal pollination through enhanced seed or fruit set/size, reduced inbreeding, and enhanced offspring viability, even when they are able to self-pollinate (Husband & Schemske 1996; Kearns *et al.* 1998; Ashman *et al.* 2004). Thus, animal pollination may enhance food production for frugivorous or seed-eating insects, birds, mammals and fish. It may contribute to the maintenance of plant diversity (Memmott *et al.* 2004), and thus to primary productivity (Tilman *et al.* 2001), which provides the vegetative cover that contributes to flood, erosion, and climate control, water purification, nitrogen fixation, and carbon sequestration (Daily 1997). No studies have yet measured how much ecosystem services provided by wild plants are increased by animal-mediated pollination (e.g. the marginal enhancement of carbon sequestration in plant communities due to increased productivity from animal pollination). Such estimations would be fraught with complications. However, it is clear that alterations of pollinator communities that affect patterns of pollen delivery will ultimately alter plant communities and the supporting services they provide (Ashman *et al.* 2004; Knight *et al.* 2005).

MARKET FORCES AND POLICY EFFECTS (7, 8)

Crop failure due to lack of sufficient pollination services can feed back via market forces to shift growers to other commodities that require fewer or no pollinators (Southwick & Southwick 1992) or to change land-use/management policies. For example, following massive applications of the pesticide fenitrothion (used for control of gypsy moth in nearby forests) in Canada, both pollinator communities and blueberry production declined (Kevan & Plowright 1989). Economic losses of blueberry growers influenced government policy, causing a virtual ban on the use of fenitrothion for gypsy moth control, and both blueberry pollinators and crop production rebounded (Tang *et al.* 2006). Shortages of honey bee colonies in 2004 for almond pollination prompted the United States Department of Agriculture to alter honey bee importation policies to allow shipments of honey bee colonies from Australia into the USA (National Research Council of the National Academies 2006). Few cases of crop yield loss due to pollination scarcity are known, however, and there is a need for better documentation of the role of pollinator scarcity in crop yield loss, and resulting policy or market responses.

Land-use policies may influence pollinator communities and pollination services through their effects on habitat quality and landscape structure at scales from single agricultural fields or woodlots to agricultural regions (8, 1). For example, the United States Farm Bill and the European Union's Common Agricultural Policy influence what crops are grown, how much land is retired from production, and

which farming practices are applied through subsidies and other incentive programs. Some programs (e.g. Agri-Environment schemes in the European Union and the Conservation Security Program in the USA, http://europa.eu.int/comm/agriculture/capreform/index_en.htm; http://www.nrcs.usda.gov/Programs/) reward farmers for a variety of putatively sound environmental practices that also influence pollinator populations (see *Case study: managing pollination services in agricultural landscapes* below). Public and private land policies, such as zoning laws, conservation easements and land trusts, also affect the amount and distribution of lands that are managed as natural, rural, suburban, urban and industrial areas, and thus the composition, density and spatial configuration of floral and nesting resources for pollinators. Some pollinator groups, notably bees, butterflies and syrphid flies, appear to be benefiting from selected agri-environment schemes (see *Case study: managing pollination services in agricultural landscapes* for details, Carvell *et al.* 2004; Pywell *et al.* 2005; Kleijn *et al.* 2006), although European agri-environment schemes and organic farming measures do not demonstrate positive results for all taxa studied (Kleijn *et al.* 2001; Hole *et al.* 2005).

Policies on control of invasive species and on importation or transportation of non-native species may influence both plant and pollinator community composition by changing the richness and abundances of non-native mutualists, competitors, herbivores, predators, parasitoids and diseases (4a,b; 5a,b; Blossey *et al.* 2001; Goulson 2003; Colla *et al.* 2006), potentially altering the interactions between the target plant and its pollinators (6B). For example, invasive pollinator species may increase the seed set and hence the spread of exotic plants (Barthell *et al.* 2001), or reduce the fitness of native plant species by reducing their nectar and pollen supplies, rendering them less attractive to other, more effective pollinators (Paton 2000). In contrast, some invasive pollinators provide substitute services to plants that have lost their native pollinators (Dick 2001). Invasive plant species may attract pollinators away from native plants (Chittka & Schurkens 2001) or crops (Free 1968), reducing seed/fruit set. Effects of a given invasive species (plant, pollinator or antagonist) are likely to be highly context-dependent; studies that either explicitly examine the role of context in determining the impacts of an invasion or factor out context to obtain more general insights (e.g. Morales & Aizen 2006) will be of greatest value.

Policies that potentially reduce or exacerbate climate change from greenhouse gas emissions may influence phenological and geographical range shifts for target plants and their pollinators, influencing whether mutualisms will persist or become spatially or temporally misaligned in the future (Parmesan *et al.* 1999; Fitter & Fitter 2002; Kudo *et al.* 2004; Gordo & Sanz 2005). To date, almost all climate change studies focus uniquely on range and phenological shifts in either plants or pollinators; future research should also target the plant–pollinator interaction, documenting potential misalignments and the reproductive and demographic consequences for plants and animals.

CASE STUDY: MANAGING POLLINATION SERVICES IN AGRICULTURAL LANDSCAPES

We illustrate the application of our conceptual framework in agricultural systems, which affects 25% of the land surface (Millennium Ecosystem Assessment 2005), influence pollinator communities (Kremen & Chaplin-Kramer in press), and rely on pollination services for a substantial fraction of global food production (Klein *et al.* 2007). How does agricultural intensification affect pollinators and pollination services and what management techniques can support pollinators and pollination services? On a local scale (BOX A), agricultural intensification can alter availability of floral resources in space and time (BOX D, 2c). It can lead to mortality or altered foraging abilities for wild pollinators due to pesticides (2B AND 4A), and to the destruction of nesting sites from tillage, irrigation and removal of woody vegetation (BOX C, 2A). On a landscape scale (BOX B, 1), intensification results in increased size of arable fields, decreased crop and weed diversity, and the loss and fragmentation of valuable natural to seminatural perennial habitats such as agroforestry systems, grasslands, old fields, shrublands, forests and hedgerows (3C).

Agricultural intensification from local to landscape scales is generally correlated with a decline in the abundance, diversity and services to crops provided by wild pollinators (reviewed in Kremen & Chaplin-Kramer in press). Thus, pollination provided by wild bees are likely being reduced in many of the areas where they could be contributing to crop production. At the same time, numbers of commercially managed colonies of *Apis mellifera* have also declined in many parts of the world (National Research Council of the National Academies 2006). Managing for wild pollinator communities and services in agricultural landscapes could help to increase the reliability of pollination services, but a full analysis of the costs and benefits (including risk management) is needed. Some studies, in contrast, show that pollinator abundance and/or diversity is higher in agricultural than in natural habitats (Westphal *et al.* 2003; Winfree *et al.* 2006). Others show that proximity to agriculture can boost pollinator abundance and/or diversity in natural habitat fragments, possibly due to floral resources provided in agricultural areas (Eltz *et al.* 2002; Winfree *et al.* 2006). Positive effects of agriculture on pollinator communities may be more likely to occur in regions where the presence of agriculture increases rather than decreases habitat heterogeneity within the foraging range of bees (e.g. < 2 km), such as farming landscapes that include relatively

small field sizes, mixed crop types within or between fields, and patches of non-crop vegetation, such as hedgerows, fallow fields, meadows, and seminatural wood or shrublands (Tscharntke *et al.* 2005).

Deliberate manipulation of plant communities is currently the best understood management tools for conserving pollination services from wild bees within agricultural landscapes. At the site level (BOX A, 2C), crops such as red clover, sunflowers, melon, oilseed rape, coffee, blueberries and almonds that provide large flushes of pollen and nectar, can help support bees and other pollinators in the short term (Westphal *et al.* 2003; Ricketts *et al.* 2004; Morandin & Winston 2005; Greenleaf & Kremen 2006b). Flower-rich field margins, set asides and permanent hedgerows can provide alternative forage for bees whose flight periods are longer than the blooming period of the crop, or attract pollinators towards relatively unattractive crops (Dover 1997; Carvell *et al.* 2004). Strip crops such as rows of coriander, intended to pull natural enemies of crop pests into crop fields, also attract pollinators (Altieri & Nicholls 2004). The specific composition of field margin, hedgerow or strip-crop plantings may be important in determining the local occurrence and population sizes of pollinators (Gurr *et al.* 2004; Pywell *et al.* 2005). Annual communities of weeds can also support bee communities on farms (Morandin & Winston 2006). At the landscape scale (BOX B, 3C), conserving perennial natural or seminatural habitats can enhance bee abundance, diversity and services on farm sites (Kremen & Chaplin-Kramer in press).

Deliberate manipulation of nesting resources is a critical complement to floral resource management (see Potts *et al.* 2005), but only a few studies have addressed this issue (e.g. Johansen 1978), due in part to the difficulty of locating bee nest sites (Kim *et al.* in press). Managing for bee nest sites can include providing: (i) patches of bare ground with soils of different textures (Handel 1997); (ii) holes of different sizes drilled into boards, fences or dead trees; (iii) standing dead trees and fallen branches; and (iv) fields where tillage (e.g. Shuler *et al.* 2005) and flood irrigation (Vaughan *et al.* 2004) are avoided. Nesting bees could be introduced in dead trees or soil plugs, as has been well worked out in the case of *Nomia melanderi* (Johansen 1978). Use of less toxic pesticides and better pesticide application procedures in intensively farmed areas would also benefit bee populations (Johansen & Mayer 1990; Vaughan *et al.* 2004; Morandin *et al.* 2005). Much work is needed to determine the relative utility of these various techniques in improving crop yields and net revenues (Olschewski *et al.* 2006), and the willingness of farmers to adopt these practices.

Although many modifications of existing farm management practices appear to increase the diversity and abundance of bees locally, it is important to distinguish between locally attractive resources that temporarily enhance bee abundance and diversity at the site, and the spatial and temporal distribution of resources that allow persistence of bee populations and diverse bee communities over time. For example, small patches of flowers potentially attract pollinators to nest in a location that cannot sustain positive offspring production over time; as such they could represent sinks or ecological traps (cf. Weldon & Haddad 2005). Similarly, while mass-flowering crops may provide substantial resources for large numbers of pollinators, they may not influence population sizes, if populations are instead limited by a bottleneck in resource abundance at another time of year (Handel 1997).

In order to restore pollination services to landscapes that have been largely transformed into intensive agriculture, studies are needed that combine multiyear, multiscale monitoring of bee abundance and pollination function in response to habitat modification; such studies could be most informative if coupled with studies of productivity and pollen resource use by selected bee species (Eltz *et al.* 2002; Williams & Kremen in press). Some important specific topics that would inform agricultural management practices are:

(1) Do flower-rich field areas (patches and field margins) compete with or facilitate crop pollination?
(2) How does diversity in floral phenology of crops, insectary plantings, agricultural weeds and native plants, affect both population persistence of bees and pollination service delivery to crops?
(3) To what extent can on-farm management practices that promote floral and nesting habitat replicate the resources provided by natural habitat?
(4) How should patches of natural habitats best be configured within agricultural landscapes to promote population persistence of bees?
(5) How do the economic costs of these management practices compare to the benefits from enhanced pollination?
(6) To what extent do these practices reinforce or detract from other services (e.g. pest control and water availability) within the agroecosystem?

GENERALIZING TO OTHER ECOSYSTEM SERVICES

A logical extension from this conceptual framework for pollination services is a general conceptual model for 'MABES' (Fig. 2). Examples of MABES other than pollination include pest control (Thies *et al.* 2005), seed dispersal (Sekercioglu 2006) and seed burial (MacMahon *et al.* 2000), vector-based disease dilution (Ostfeld & LoGiudice 2003), decomposition (Larsen *et al.* 2005; Losey & Vaughan 2006), nutrient deposition and ecosystem engineering (Sekercioglu 2006). This conceptual framework
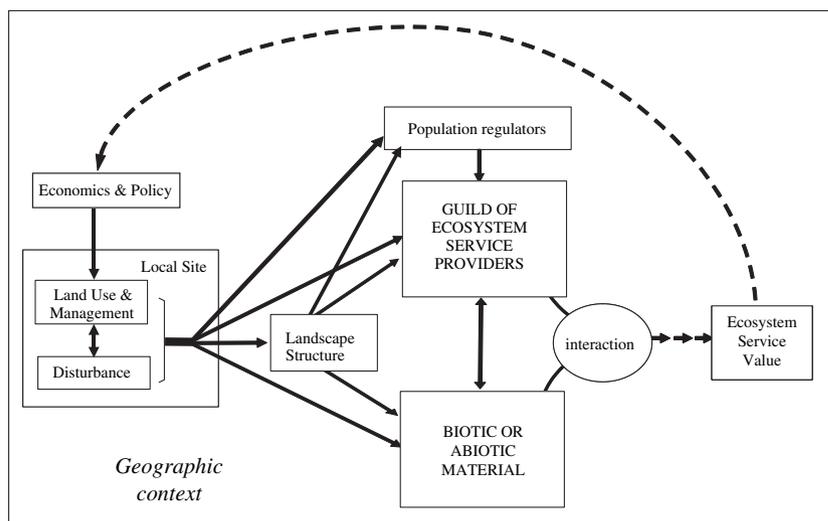
Figure 2 Generalizing the conceptual framework to other mobile agent-based ecosystem services.

for MABES builds on that of 'mobile-link species' (Gilbert 1980) by extending it to include not only basic ecological functions in natural habitats, but also ecosystem services in changing, human-modified landscapes. The salient features of this generalized model, which is directly analogous to the more specific model for pollination services (Fig. 1) are that: (i) local and landscape level management practices create the conditions that influence mobile agents, their population regulators, and the biotic community or abiotic/biotic material with which the mobile agents interact; (ii) the result of these interactions produces the service, which produces goods of value to humans, or influence the outcomes of other ecosystem services; (iii) ecosystem service values feedback via market-based forces to influence land-use and management policies; and (iv) these policies in turn influence land-use and management practices that create both local site conditions and landscape structure.

Although MABES tend to be delivered at a local scale, the mobile agents themselves often come from and/or are influenced by a larger, service-producing area (Lundberg & Moberg 2003). For any point in the landscape, the value of services provided by mobile agents derives from the region within foraging or dispersing distance of the point of delivery. As described in detail for pollination services, the qualities of the landscape around a site, as well as the local environment at the site, will influence the distribution of resources and habitat for mobile agents, and thus service delivery (e.g. pest control, Thies *et al.* 2005). Patches of wild and seminatural habitats may be critical for maintaining diverse and abundant communities of mobile agents, but the anthropogenic matrix may also supply important resources that both contribute to population persistence of mobile agents and help to attract them, thereby delivering services into the matrix. While many ecosystem services share the property of being influenced by a larger service-producing

landscape (e.g. water-based services), MABES are distinct in that the scale of production and delivery of the service is set primarily by the mobility of the service-delivering organisms (Kremen 2005). In contrast, the scale of other services may be set primarily by physiographic features such as watershed topography, or be global in scale, such as climate change mitigation by carbon sequestration and storage.

The services provided by a given community of mobile agents are highly contextual. They may be influenced by either the composition of the mobile agent community and/or the recipient community (at least for services produced by the interaction between mobile agent and recipient, such as parasitoid – pest), through alterations in the effectiveness of individual species in differing community contexts (Kremen 2005). For example, a disease host that transmits its disease infrequently to a vector can dilute the disease if more competent hosts co-occur, but may become the main source of the infection if it is the most competent host in the community (Ostfeld & LoGiudice 2003). Competitive or facilitative interactions between species can alter functional outcomes (e.g. pest control, Cardinale *et al.* 2003; decomposition, Jonsson & Malmqvist 2003). Context (community composition) is altered in turn by changes in landscape structure that affect non-random community assembly/disassembly processes. For example, small fragments of forest in the northeastern USA have lost many of the least competent vertebrate hosts for the vector of Lyme disease, resulting in less disease dilution and higher Lyme disease infection risks in humans (Allan *et al.* 2003; Ostfeld & LoGiudice 2003). Non-MABES ecosystem services can also be influenced by context; for example, trees in the Australian landscape provide water filtration services, while in a South African landscape, they reduce groundwater discharge, a negative environmental service (van Wilgen *et al.* 1998; Eldridge & Freudenberger 2005).

We began by creating a conceptual model of a single MABES, pollination. Such a conceptual model helps to reveal knowledge gaps that currently impede development of effective management plans for the service. We encourage workers on other MABES to utilize the generalized conceptual framework similarly for development of research priorities and management alternatives in their own systems. These management alternatives could then be implemented in an experimental, hypothesis-driven framework, by gathering data that could feedback to strengthen the conceptual model, evaluating the ecological and economic consequences of the management choice, and adapting the management plans accordingly (Walters & Holling 1990). A further challenge is to integrate across services in evaluating tradeoffs and synergies of alternative management schemes.

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