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Review

Pollinator habitat enhancement: Benefits to other ecosystem services

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ABSTRACT

A range of policy initiatives have been promoted in recent years to address the decline of bee populations in Europe and North America. Among these has been the establishment of flower-rich habitat within or around intensively farmed landscapes to increase the availability of pollen and nectar resources. The composition of these habitats depends on location and compatibility with adjacent cropping systems, but they often consist of fields planted with temporary flowering cover crops, field borders with perennial or annual flowering species, hedgerows comprising prolifically flowering shrubs, and grass buffer strips (used to manage erosion and nutrient runoff) which are supplemented with dicotyledonous flower species. While the primary objective of such measures is to increase the ecological fitness of pollinator populations through enhanced larval and adult nutrition, such strategies also provide secondary benefits to the farm and the surrounding landscape. Specifically, the conservation of pollinator habitat can enhance overall biodiversity and the ecosystem services it provides (including pest population reduction), protect soil and water quality by mitigating runoff and protecting against soil erosion, and enhance rural aesthetics. Incorporating these secondary benefits into decision making processes is likely to help stakeholders to assess the trade-offs implicit in supplying ecosystem services.

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1. Introduction

In recent years, substantial declines in the abundance and diversity of insect pollinators have been widely documented (Ghazoul, 2005; Steffan-Dewenter et al., 2005; Biesmeijer et al., 2006; Williams and Osborne, 2009). While much of that attention has focused on managed honey bees (*Apis mellifera* L.) and the condition called Colony Collapse Disorder (Oldroyd, 2007), various wild bee species have also suffered serious declines (Biesmeijer et al., 2006; Potts et al., 2010) and in some cases have disappeared from their historic natural ranges (National Research Council, 2007; Cameron et al., 2011).

The loss of these pollinators is likely to have serious consequences for both general biodiversity and crop productivity (Kevan and Phillips, 2001). Pollinators are essential or beneficial for the production of many crop species (Southwick and Southwick, 1992; Williams, 1994; Westerkamp and Gottsberger, 2000; Klein et al., 2007), and they are also important for the reproduction of more than 65% of the world's wild plants (Kearns et al., 1998; Ashman et al., 2004). Globally, they are responsible for pollinating approximately 30,000 plant species (Buchmann and Nabhan, 1996) with a third of human food consumed benefitting directly or indirectly from this ecosystem service (McGregor, 1976). The annual global value of animal-mediated crop pollination is estimated at $153 billion (Gallai et al., 2009).

A single factor has not been identified to explain the decline of managed and wild bees, but rather multiple issues are likely to be involved. These include the degradation and fragmentation of natural habitat (Richards, 2001; Kremen et al., 2002; Larsen et al., 2005), the loss of flower-rich plant communities associated with traditional landscape uses such as heathlands and legume-based set-aside fields (Goulson et al., 2008; Kleijn and Raemakers, 2008), the spread of pathogens and parasites (Potts et al., 2010) and the widespread use of agricultural pesticides (Kevan, 1975; Desneux et al., 2007). However, a meta-analysis (Winfree et al., 2009) of studies assessing these threats found that habitat loss was the human activity most significantly detrimental to the abundance and diversity of bees, particularly in extremely disturbed landscapes. Similarly, a growing body of research has demonstrated that farms located in close proximity to natural areas can receive all of their pollination services from wild bees alone (Kremen et al., 2002, 2004; Winfree et al., 2007). Research has also shown that the frequency of crop flower visits by pollinating insects (a predictor of actual pollination, Vázquez et al., 2005) and subsequently crop yield are higher in areas located closer to natural or semi-natural habitats (Ricketts et al., 2004; Chacoff and Aizen, 2006; Blanche et al., 2006). These studies highlight that less fragmented landscapes with some intact natural habitat are beneficial to bee populations and that agriculture can play an important role in addressing bee and general biodiversity declines through thoughtful management. However, recognizing the value of at least some of the habitat diversity outside the crop raises at least two questions: (1) which aspects of non-crop habitat are most important? (2) Can this information be developed for practical use by land owners and others, i.e., a Service Providing Unit (SPU; Luck et al., 2003)?

In recognition of the above findings, the United States Department of Agriculture (USDA) and the European Union's Agri-Environmental Regulation Initiative have promoted various Agri-Environmental Schemes (AES) (Whittingham, 2011) which encourage the creation of flower-rich habitat in the form of hedgerows, field-border plantings, temporary flowering cover crops and flower-rich buffer strips. These conservation strategies are often supported with direct financial subsidies and technical advice for their design, implementation, and ongoing management (Decourtye et al., 2010; Farley and Costanza, 2010).

The success of these schemes has been varied however (Kleijn and Sutherland, 2003; Kleijn et al., 2006), and may depend on acceptance and popularity to farmers and the public (Haaland et al., 2011). Furthermore, it is difficult to successfully link the enhancement of pollinator habitat adjacent to crop fields with increased yield, a factor that may affect widespread adoption of such practices by farmers. In fact, despite positive effects of adjacent natural habitats (above), and records of increased pollinator abundance and flower visitation, there is a lack of research documenting pollination spill-over in the other direction, i.e., into crops from flower rich margins or from 'pollinator-enhancement' strategies (although see Hoehn et al., 2008). This in turn can create difficulties in grower acceptance due to a perceived potential conflict between crop productivity and biodiversity conservation (Power, 2010).

Beyond the direct benefit to pollinators however, AES efforts targeting the conservation of bees may yield additional value. Here we attempt to identify some of the secondary benefits of pollinator habitat enhancement, including the protection of general wildlife biodiversity, the enhancement populations of other beneficial insects (those that prey upon or parasitise crop pests), the protection of soil and water quality, and the enhancement of rural aesthetics. A similar effort was made by Fiedler et al. (2008) in relation to the multiple benefits of habitat manipulation for conservation biological control of pests. In this review, we hope to add to this earlier work and that by synthesizing the multiple ecological, economic and aesthetic benefits of pollinator conservation, to be able to demonstrate the wider importance of such management.

2. Background: pollinator habitat enhancement

The enhancement of pollinator habitat on farmland can take a number of forms, although the most often studied management techniques consist of field margin manipulation, including non-crop buffer strips which can provide nesting sites and encourage forage plant growth, the restoration of native plants in adjacent natural areas, wildflower strips sown with pollen- and nectar-rich plants, or a mixture of all three (Decourtye et al., 2010; Haaland et al., 2011). Hedgerows may also be valuable as they can provide a sheltered habitat for a number of native and woodland adapted and woodland edge plant species (Boutin and Jobin, 1998; Corbit et al., 1999). The reintroduction of crop rotation, grassland leys and legume rich set-aside land is also recommended in a number of agro-ecosystems, as well as cover crops in orchards for example (Altieri, 1999).

The success of the different techniques has been mixed. A number of studies assessing the impact of enhancing floral resources on farmland have shown that bee abundance and diversity is positively correlated with the abundance and diversity of floral resources (Ostler and Harper, 1978; Steffan-Dewenter and Tscharntke, 2001; Kleijn et al., 2004; Hagen and Kraemer, 2010). Studies have also shown that peripheral areas around crops containing varied wildflower species have positive effects on the abundance and diversity of many insect pollinators such as honey bees, bumble bees, butterflies, syrphidae and other dipterous insects (Lagerhöf et al., 1992; Carreck and Williams, 1997; Cheesman, 1998; Backman and Tiainen, 2002; Croxton et al., 2005). The extent to which increasing local pollinator abundance increases long-term ecological fitness and enhances crop pollination rates is less certain. However, there are parallels with the use of flowers to enhance the efficacy of pests' natural enemies, particularly parasitoids. In the latter case, a hierarchy of consequences of flower deployment can be expected (Gurr et al., 2003). This hierarchy is summarized in Fig. 1. For pollinators on farmland, a hierarchy could be as shown in Fig. 2.

Finally, it is important to note that among forage-enhancement strategies for pollinator conservation, some plant mixes may

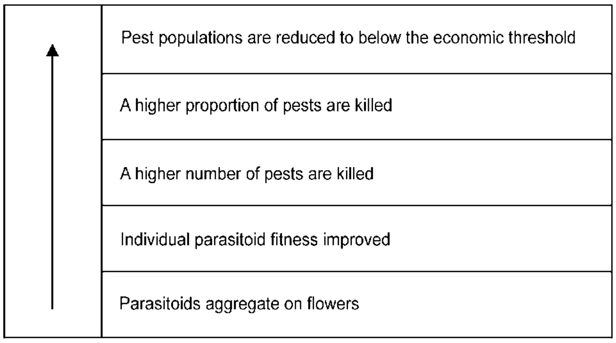

Fig. 1. A hierarchy of possible effects on parasitoids of pest insects when flowers are deployed in an agro-ecosystem. The arrow indicates the trend in the value of the effect as well as the difficulty of achieving it.

contain redundant species (Carvell et al., 2006), omit some beneficial species (Pywell et al., 2005) and like AES in general, may simply increase populations of already common pollinator species (Haaland et al., 2011). Natural regeneration of plants can be unpredictable (Carvell et al., 2004) leading to establishment failure, or to the growth of pernicious weeds (Pywell et al., 2005). This can be a problem because the success of AES schemes depends on the persistence of high value flower species in the seed bank (Firbank et al., 1993; Goulson et al., 2008). The importance of wildflower strips may also depend on their subsequent management (Haaland et al., 2011). Nonetheless, as a result of the attention given to pollinator habitat enhancement strategies, the scientific community is beginning to understand more about the important factors involved in targeting certain pollinators. Some of these are considered here.

2.1. Impact of floral diversity on pollinators

While some pollinators benefit from the mass flowering of certain crops (e.g. *Bombus* spp./oilseed rape; Westphal et al., 2003),

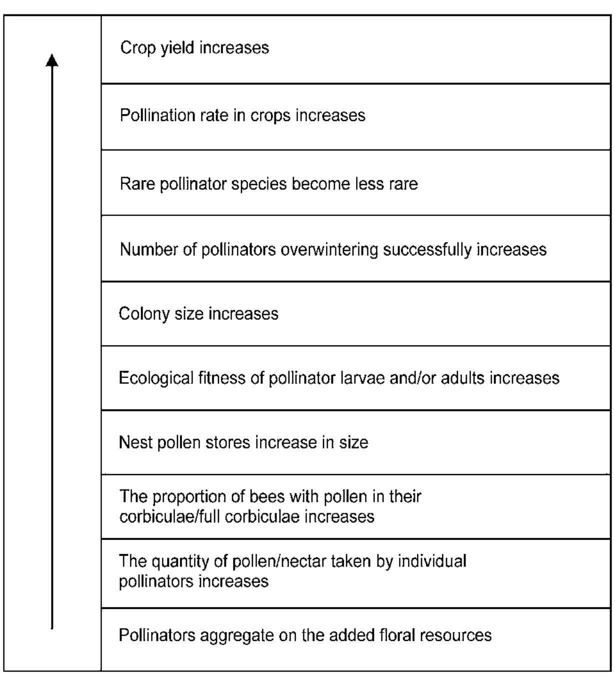

Fig. 2. A proposed hierarchy of the effects of deploying flowers in farmland to enhance pollinator fitness and effectiveness. Benefits to other farmland ecosystem services can accrue at any point on this hierarchy.

the importance of such monocultures to pollinators is poorly understood, particularly with respect to the wider landscape and long-term pollinator fitness (Hanley et al., 2011). These flowering episodes also tend to be temporary, occurring in a fraction of the active season of many bee species. Evidence is also beginning to demonstrate that floral diversity is important in the population enhancement of polylectic species (Carvell et al., 2004; Pywell et al., 2005), in ensuring stability of pollinator population densities (Ghazoul, 2006) and in enhancing the diversity of pollinator communities (Greenleaf and Kremen, 2006; Ebeling et al., 2008; Winfree et al., 2008). Community level studies have shown that maintaining the structure of the entire food web is important because a greater diversity of pollinators, and of pollination guilds, can improve yield (Hoehn et al., 2008) and because rare plants may be linked to common plants through shared pollinators (Gibson et al., 2006). In addition, a diverse range of pollinators is vital to ensuring that declines in honey bee populations are buffered (Westerkamp and Gottsberger, 2000; Greenleaf and Kremen, 2006).

With these factors in mind, pollinator habitat enhancement aims to provide a diverse and continuous succession of alternative food sources that ensure the persistence of bee populations throughout the year (Pywell et al., 2005; Carvell et al., 2006; Goulson et al., 2008). This is also likely to benefit the next generation of pollinators. For example mixtures of diversified perennial wildflowers that consist of successively flowering species will provide greater continuity of foraging resources than will other mixtures primarily made up of species in the Fabaceae for example, especially early in the season (Carvell et al., 2007) when queens of social species are foraging to establish new colonies (Fussell and Corbet, 1992).

2.2. Links between floral abundance and pollinator nutrition

The survival and development of honey bee colonies is influenced by the regularity, quality and quantity of nectar and pollen: (1) after over-wintering for the replacement of workers; (2) during spring and summer when the population has peaked, and; (3) in autumn for the storage of winter food. Floral resource gathering during the main honey bee season must be sufficient to feed 50,000 workers and 9000 larvae, for example. An average colony may have an annual nectar requirement of about 120 kg and a pollen requirement of 20 kg (Seeley, 1995) and a colony may stock between 60 and 80 kg of honey per year (Seeley, 1995), with 15–30 kg of (non-surplus) honey per colony for its own consumption. The highest consumers of pollen are the nurse worker bees of social bee colonies which eat large quantities of pollen: 60 mg over 10 days (Pain and Maugenet, 1966), to fuel the secretory glands which produce food for larvae, and larvae consume 42 mg during the first 5 days of development (Haydak, 1970). This food source from the workers constitutes a major part of the larval protein supply.

Pollen abundance is also important for wild bees. For example, although the solitary bee *Megachile parietina* Geoffroy is polylectic, it prefers to feed from *Onobrychis viciifolia* Scop and Muller et al. (2006) found that a female bee of this species required the pollen content of 1139 individual flowers of the preferred species to rear a single offspring. Oligolectic species with similar demands will require a great abundance of their preferred food plants, and it has been suggested that populations of some species with a narrower diet breadth have declined more than have generalist species (Kleijn and Raemakers, 2008; but see Connop et al., 2010), in line with declines of their preferred plants (Biesmeijer et al., 2006). Conversely, wildflower abundance is positively correlated with pollinator diversity in a number of systems (Klein et al., 2003; Potts et al., 2006; Hagen and Kraemer, 2010), and pollinator abundance to blossom density (Steffan-Dewenter and Tscharntke, 2001; Ebeling et al., 2008).

2.3. Importance of flower species selection

While it may seem intuitive that a greater diversity of flowers results in a diverse community of pollinators, the positive effect of flowering areas on bees depends on the plant species available (Carreck and Williams, 1997; Cheesman, 1998) and their accessibility to local bee communities. For example, some farmland weeds, typical of disturbed areas, such as cleavers (*Gallum aparinel* L.), common knotweed (*Polygonum aviculare* L.) and twitch (*Alopecurus myosuroides* Huds.) in the UK, are not used by foraging bees (Pywell et al., 2004). Even among suitable herbaceous flowering plants that are used by bees, floral morphology can influence the abundance and diversity of pollinators. For example, species such as *Bombus lucorum* L. and *Bombus pratorum* L. have short tongues (7 mm) that are adapted to forage on short open flowers (Asteraceae), whereas *Bombus hortorum* L. has a longer tongue (13 mm) enabling the bee to feed on flowers with long corolla tubes such as *Trifolium pratense* L. (Prys-Jones and Corbet, 1991). Therefore a legume-rich border or fallow field will attract mostly long-tongued species, and a farmer growing crops such as field beans in the UK is likely to benefit from this specific pollinator enhancement (Fussell and Corbet, 1992).

In the USA, native legumes (such as *Dalea* spp. and *Lupinus* spp.), Asteraceae (e.g. *Silphium* spp., *Solidago* spp., *Symphyotricum* spp.), and Lamiaceae (e.g. *Agastache* spp., *Monarda* spp., *Pycnanthemum* spp.) are considered particularly important pollen and nectar sources for both wild and managed bees (Mader et al., 2011). However, the identification of important plants is often dependent on region, local pollinator species composition, landscape history and other habitat factors (Tuell et al., 2008; Connop et al., 2010; Menz et al., 2011), particularly as plants selected in one country or state may become weeds in another (Winfree, 2010). Similarly, while the Tübingen mix developed in Germany is effective in supporting honey bee and wild bee populations in temporary bee pastures (Engels et al., 1994), when tested in the UK, the mixture was considered inappropriate as species' flowering times coincided with those of major crop-forage sources and therefore attracted few insects (Carreck and Williams, 1997). Future species selection should perhaps follow a protocol for identifying and testing regionally important forage plants, such as that developed in the USA and successfully introduced to Central Asian countries (Isaacs et al., 2009). This protocol involves the screening of plant species native to the focal region in replicated trials for the abundance of pollinators and natural enemies of pests visiting them. High ranked species are then selected for planting schemes based on overlapping blooming periods to ensure constant forage availability through the active season of beneficial insects (Isaacs et al., 2009).

Overall, the success of pollinator habitat enhancement through the addition of forage plants will depend on more than the flowers themselves. Factors such as the abundance of nesting habitat and the foraging range of pollinators will interact to determine the required abundance of food plants. The impacts of land management, landscape heterogeneity and the proximity of natural habitat, should not be underestimated either. These factors are beyond the scope of this paper, but an excellent review is provided by Roulston and Goodell (2011).

Our understanding of pollinator nutrition, of the importance of flower species and floral continuity and of the links between floral abundance and diversity and pollinator populations has advanced greatly in the past few decades. When this knowledge is applied to the agro-ecosystem, many of these factors can also benefit other aspects of farm management and agro-ecological conservation. These are considered in the next section.

3. Additional ecological, economic, and aesthetic benefits of floral enhancement for pollinators

In this section we discuss how the incorporation of flowers into farmland may support other ecological services. Both primary and secondary benefits are summarized in Fig. 3, using a hierarchy of scale adapted from Gurr et al. (2003) in their review of multi-functional benefits produced by enhancing agricultural biodiversity for pest management. This hierarchy illustrates benefits at the level of the plant, crop, farm and landscape. However, in the next section we also highlight the potential problems with this approach, acknowledging the costs involved in pollinator habitat enhancement and the difficulties associated with evaluating the differing temporal and spatial aspects of these ecosystem services.

3.1. Biodiversity conservation

The obvious beneficiaries of non-crop flowering areas are the plant species being promoted with rare species in particular likely to benefit from the conservation of their pollinators (Gibson et al., 2006). As native plants are beginning to form the focus of some pollinator restoration efforts ahead of introduced species (Isaacs et al., 2009; Menz et al., 2011), this is likely to benefit native plant communities and the fauna associated with them. A parallel approach in New Zealand deploys endemic flowering plant species to complement or replace non-native species in vineyards. The aim of this work is to provide nectar for predators and parasitoids of vine pests (Fiedler et al., 2008; Tompkins, 2009).

The incorporation of flowering plants into non-cropped farmlands also has the potential to help restore habitat for many non-pest insects, such as many butterflies, in intensively farmed areas. The result is a cascade of effects at the farm and landscape level, which can help to mitigate threats to insect biodiversity on farmland including habitat loss, encroachment by invasive plant species, and pollution (Tilman et al., 1994; Thomas et al., 2004; Clavero and Garcia-Berthou, 2005). For example, non-cropped habitats can provide winter refugia for many insects that can repopulate adjacent agricultural lands during favorable conditions (Wratten, 1988; Thomas et al., 1994; Wade et al., 2008). Furthermore, as the structure of non-cropped farmlands influences insect distribution and diversity, management tactics targeting enhanced plant biodiversity have the potential to increase general insect biodiversity and to decrease the potential for extinction of rare species (Bianchi et al., 2006). Among such management tactics, field studies conducted in Sweden demonstrated that the presence of wild plants in agricultural areas facilitated the persistence of a broad diversity of insects (Lagerhöf et al., 1992; Lagerhöf and Wallin, 1993).

In addition to invertebrates, non-cropped areas have been identified as providing habitat for birds and mammals. Researchers in the state of Louisiana, USA, documented extensive use of non-cropped areas as movement corridors for black bears (*Ursus americanus* Pallas) between fragmented woodlands. The researchers noted that radio collared female bears only moved between wooded areas separated by agricultural lands when non-cropped corridors were present (Henry et al., 1999). In the UK, the seeds of some insect pollinated arable plants are an important food source for bird species (Marshall et al., 2003), and game birds and mammals benefit from insect diversity and abundance in 'beetle banks' (Boatman, 1999; Thomas et al., 2001) and conservation headlands (Dover et al., 1990).

3.2. Conservation biological control

Conservation biological control is a valuable ecosystem service (Losey and Vaughan, 2006) but intensive agriculture (e.g.

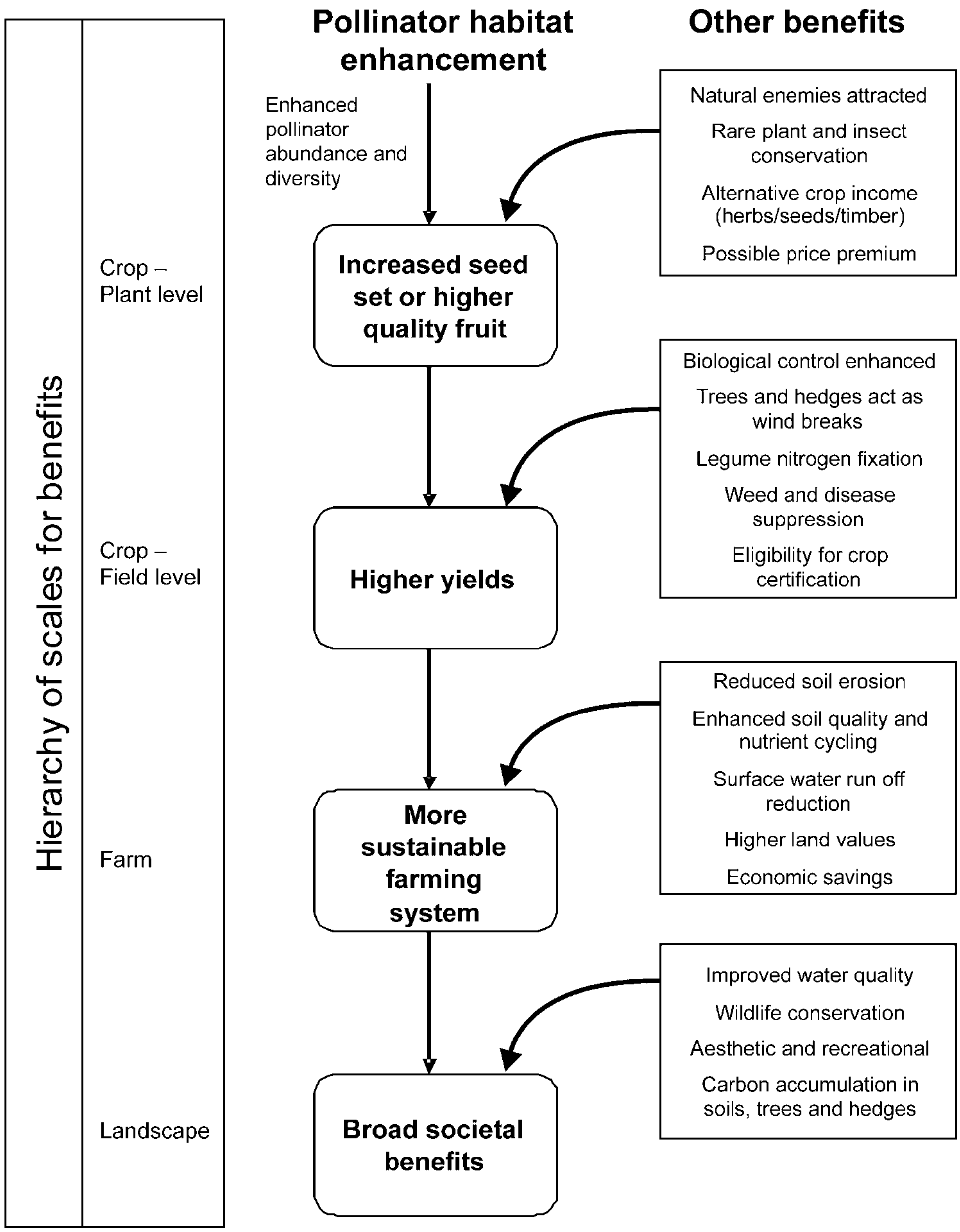

Fig. 3. A hierarchy of scales for potential benefits of pollinator habitat enhancement.

Adapted from Gurr et al. (2003).

simplification of landscape structure) strongly affects natural enemy populations and the biocontrol services they provide (Chapin et al., 2000). Landscape biodiversity management and restricted used of pesticides can help enhancing biocontrol services in agro-ecosystems (Winqvist et al., 2011; Lu et al., 2012). It is increasingly recognized that greater plant diversity within farmland (Thies and Tscharntke, 1999; Landis et al., 2000; Lundgren et al., 2009) and the presence of non-cropped areas in agricultural landscapes can help to sustain populations of natural enemies of pests (Landis et al., 2000; Marshall and Moonen, 2002). The value of naturally occurring insect predators and parasitoids has been estimated at $4.5 billion annually in the United States based upon the value of crop losses as well as the cost of insecticides (Losey and Vaughan, 2006). Specifically, hedgerows and other non-cropped habitats support greater numbers of beneficial arthropods than do simple landscapes (Holland and Fahrig, 2000; Lee et al., 2001; Pollard and Holland, 2006), and intentionally planted wildflower areas have been developed successfully as reserves of natural enemies (Thomas et al., 1991). In some cases such reserves translate directly into pest population suppression. For example in a review, Bianchi et al. (2006) found that pest pressure was reduced in 45% of such studies. These reductions include both pest densities (Ostman et al., 2001) as well as crop damage (Thies and Tscharntke, 1999; Thies et al., 2003). The plants selected as floral resources for pollinators also may enhance establishment of biological control agents which are released against arthropod pests (Gurr and Wratten, 1999). For example, *Phacelia tancetifolia*, a native plant in the USA, supports natural enemies of pests (Berndt et al., 2006). This species is also useful to pollinators such as bees, flies and butterflies (Carreck and Williams, 2002).

Thus, making small adjustments in the management of non-cropped habitats, such as adding nectar-producing plants, can combine the benefits of biodiversity and pest-control, thereby optimizing overall ecological services. It is important to note however that additional food resources selected to enhance pollinator or natural enemy populations may also enhance pest populations (Wäckers et al., 2007; Parolin et al., 2012). For example, some nectar resources are used by both natural enemies and pests (Baggen and Gurr, 1998; Lavandero et al., 2005). Therefore, research is needed on the effect of specific plants on natural enemy and pest fitness (e.g., longevity and fecundity) and to ensure that 'selective biodiversity' is deployed. The results of this type of work can be subtle because (a) although pest fitness may be increased with some floral resources, it may be a relatively smaller effect than on target natural enemies. Modeling such as that by Kean et al. (2003) can help evaluate the population and community consequences of this; (b) pest longevity may increase but there may be no consequent effect on fecundity. This was the case for the diamondback moth (*Plutella xylostella* L.), while longevity and fecundity both increased for its parasitoid *Diadegma semiclausum* (Hellén.) (Lavandero et al., 2005). These subtleties are likely also to apply to pollinator dynamics, such as in relation to the hierarchy suggested in Fig. 2.

3.3. Soil and water quality protection

Managing non-cropped farmlands as pollinator habitat could benefit overall soil quality. At the crop and farm level, permanent vegetation cover helps limit soil erosion (Nearing et al., 2005), and absorbs excess soil nitrogen that might otherwise be leached below the root zone of plants in the soil profile (Meisinger et al., 1991; Justes et al., 2004). In addition, many pollinator-friendly leguminous cover crops fix atmospheric nitrogen into their biomass (via symbiotic associations), with positive effects on soil fertility, reducing the need for synthetic fertilizers because nitrogen is progressively released back into the soil (Mary et al., 1999; Thönnissen et al., 2000). In addition, grasses inter-planted with leguminous plants absorb a portion of nitrogen, storing it for later release when the grass is mowed (Huntington et al., 1985). Thus, mixtures of grasses and legumes planted along field margins could provide both extensive foraging and nesting opportunities for pollinators, natural enemies of crop pests, birds, mammals and benefits to soil fertility.

Soil structure and compaction can be addressed by temporary pollinator-friendly cover crops (e.g., *Raphanus sativus* L., *Brassica napus* L., *Medicago sativa* L.) that increase organic matter (making the soil more porous) before planting the following year's crops. At the landscape level, pollinator-rich hedgerows and wildflower field borders may also protect water quality by reducing surface water run-off (potentially containing pesticide and/or fertilizer residue) into drainage ditches and streams. Depletion of nitrogen, phosphorus and potassium in agricultural soils often requires substantial inputs of synthetic fertilizers which are often associated with negative environmental side effects (notably water pollution, Rohr et al., 2008). Buffer strips consisting of permanent non-cropped vegetation can remove up to 97% of soil sediment before it enters adjacent streams (Lee et al., 2003; Lowrance et al., 2002), and to reduce the concentration of nitrogen from between 40 to 94% before it enters adjacent surface water (Lovell and Sullivan, 2005).

3.4. Weed suppression and weed control savings

The planting of certain non-crop flowering species can also help to suppress weeds. For example, in New Zealand, low growing native shrubs planted beneath grape vines with the purpose of providing nectar to natural enemies of pests, also suppressed exotic weeds (Tompkins, 2009). The use of mixtures with grass and certain flowering plants to attract insect pollinators has also been suggested as providing the additional benefit of suppressing pernicious agricultural weeds such as *Cirsium* species (Smith et al., 1999; Pywell et al., 2005). The maintenance of a perennial flora may therefore help to reduce the competitiveness of annual weed species, reduce the level of disturbance associated with this management and can help to manage weed ingress into the crop (Moonen and Marshall, 2001; Marshall and Moonen, 2002). The encouragement of flower-rich field margins and the education of farmers on the benefits of some non-crop species should also lead to a decrease in the intensity of chemical control and savings associated with fewer chemical inputs.

3.5. Rural prosperity and aesthetics

A recent survey reported that more than one-third (39%) of the people surveyed chose ecotourism opportunities as their first vacation preference (Perkins and Grace, 2009). Interest in agritourism, a branch of ecotourism, is also increasing in the US and EU (Burger, 2000; Carpio et al., 2008; Saxena and Ilbery, 2008) with restoration of traditional landscapes increasingly prioritized for tourism and scenic value (Meeus, 1993). Bird-watching, hiking, backpacking, and primitive camping are four of the fastest-growing recreational activities in the USA (Cordell et al., 1999) most of which are associated with rural settings. Enhancing those settings with large and diversified colorful flowering plants that attract pollinators could provide equally attractive sites with tourist potential. Similarly, in the United States and parts of Europe, hunting can be a significant source of income for farmers who lease larger non-cropped areas. For example, field windbreaks in the state of Kansas generated an annual net income of $21.5 million from leasing the land to hunters (Henry et al., 1999). Agrotourism may thus fulfill the expectations of many ecotourists where the implementation of AES measures support greater biodiversity and make rural landscapes more attractive.

In New Zealand, a project called 'Greening Waipara' has identified the aesthetic benefits to ecotourism from improving biodiversity on farmland. The project encourages and assists vineyard owners in the Waipara region of northern Canterbury to plant once common native plant species to enhance 'stacked' ecosystem services including pest and weed control. In addition, visitors to the region can learn about the benefits of native plants along hiking trails which start close to the wineries and restaurants of some vineyards (Fiedler et al., 2008). These trails are considered by tourists to be a positive addition to otherwise monocultural vineyard landscapes and leads to a greater 'brand reach' for their products (Forbes et al., 2009).

Agritourism is also increasingly associated with broad concepts of sustainability (Loumou et al., 2000) and for some farmers can be an important income-generating concept in marketing their crops (Oppermann, 1996; Barbieri and Mahoney, 2009). Making rural areas attractive for agritourism can bolster regional economics while protecting land and biodiversity on a large scale (Burger, 2000). The few studies conducted on rural land aesthetics have demonstrated a visual preference of visitors for the presence of non-cropped areas in farm landscapes (Lovell and Sullivan, 2005), with some agricultural lands that include wildlife habitat commanding higher prices per hectare (Bastian et al., 2002).

4. Assessing the economic benefits of pollinator habitat enhancement

Despite the clear practical benefits of enhancing pollinator habitat to other species and aspects of agriculture, making changes to farm architecture may often require capital outlay, a change in farm practices and recurring or hidden costs such as habitat maintenance (Table 1). Many landowners may be reluctant to undertake such changes. For example, despite apparent economic benefits, less than 1% of global pest control sales are related to biological control (Griffiths et al., 2008). Decisions to adopt alternative techniques may be based on social, cultural and environmental factors

Table 1
Obvious and less obvious costs and benefits of enhancing pollinator habitat.

Costs	Benefits
Obvious factors	
• Loss of cultivated land and corresponding crop yields • Potential loss of yield due to variability of wild pollinators • Costs of restoring non-crop vegetation (flower seeds, specialised machinery) • Labour	• Small savings in production costs by reducing the size of cultivated land • Savings in honeybee hive rental fees • Potential subsidies from agri-environment schemes or price premiums for organic or 'environmentally friendly' products
Less obvious, delayed or non-monetary factors	
• Training of habitat enhancement techniques • Monitoring enhancement areas for successful establishment of flowers and beneficial insect populations • Maintenance costs of new habitats • Increase in pests attracted to wildflowers • Increase in weeds • Increase in diseases • Possible lack of spill-over (pollinators are attracted to wildflower margins and do not enter crop)	• Increase in biological control – reduction in pesticide use • Reduced pesticide decreases likelihood of resistance developing • Landscape manipulation helps other ecosystem services • Increased soil fertility • Suppression of weeds • Alternative crop potential – sale of wildflower seeds or timber • Aesthetic value of improved landscape • Improved water quality • Improved plant and insect conservation • Other wildlife benefits • Community benefits beyond farm boundary

Adapted from Gillespie and Wratten (2012).

(Jackson et al., 2007), how landowners learn about and adopt new practices (Cullen et al., 2008), and policy and incentive support systems (Falconer and Hodge, 2000), as well as economic efficiency. In addition, ecosystem services may operate or accumulate at different spatial and temporal scales, making economic valuation difficult. For example, while improving some ecosystem services may provide early financial compensation to the farmer or society (attraction of natural enemies and pollinators to flower strips), others will incur some losses before the benefit is truly enjoyed (hedgerows take years to mature, soil nutrient cycling may take many seasons to improve). The lack of short-term financial benefit may prevent some farmer uptake, and current cost–benefit analysis tools may fail to take into account the local and regional trade-offs involved in selecting ecosystem service enhancements.

Nevertheless, demonstrating the economic value of ecosystem services such as pollination and biological control is seen as a useful way to frame their importance to non-ecologists and policy makers (Costanza et al., 1997; Losey and Vaughan, 2006). Also, 'packaging' information in the form of Service Providing Units (Luck et al., 2003) is a very important step in achieving outcomes. The total value of these multiple secondary benefits incurred through habitat enhancement is often ignored by farmers in economic decision making (Jackson et al., 2007). Taking account of the full range of benefits and costs highlighted in Table 1, as well as the temporal and spatial scales over which they operate may assist farmers in making true cost–benefit analyses, and may assist policy makers in establishing accurate financial incentives to encourage AES adoption (Fiedler et al., 2008).

The valuation of many interconnected ecosystem services is not an easy undertaking, especially because they are often not easily convertible to a common measurement unit such as price (Gomez-Baggethun et al., 2010). There have been attempts to value multiple benefits of insect conservation such as Losey and Vaughan's (2006) valuation of crop pollination by wild bees in the United States at US$3 billion annually, and insects generally at US$57 billion. However, it is difficult to model any potential increase of that value in relation to broader adoption of habitat enhancements. Assessing such economic impacts is likely to require distinct valuations of component parts, a process that may suffer from difficulties such as the potential for over-valuation through the double counting of benefits (El Serafy, 1998; Fu et al., 2011) and uncertainty about the interconnected nature of ecosystem services (Diaz et al., 2007). For example, pollinators and other organisms do not distinguish between field boundaries making counting units difficult to discern (Zhang et al., 2007) and some species typically perform more than one function (Diaz et al., 2007; e.g. hoverfly larvae consume insect pests and as adults are pollinators).

Nonetheless various economic modeling systems for distinct ecosystem services do exist, and while the resulting data tend towards case-specific values, these modeling approaches could provide the foundations for a more comprehensive economic analysis of the secondary benefits provided by enhancing pollinator habitat. For example, Cullen et al. (2008) propose a six-step cost–benefit analysis for conservation biological control projects in which: (1) a private, national, or global 'perspective' is selected to determine whether local or global prices and costs are used; (2) an evaluation time frame is established; (3) physical consequences including inputs and outputs are listed; (4) the monetary value of those inputs and outputs is estimated (cost and benefits); (5) costs and benefits are compared, and discounted as necessary (such as to include government financial incentive programs); (6) the results are summarized. If the benefits exceed total costs, and if they extend beyond a single year, net present value (NPV) can be calculated:

$$\mathrm{NPV} = \sum_{i=1}^{n} \frac{Bi - Ci}{(1+d)^i}$$

In which *Bi* are benefits, *Ci* are costs, *d* is the discount rate, and *i* is the project year.

Direct market valuation of secondary benefits provides another approach to modeling the economic impact of pollinator habitat enhancements. Barbour et al. (2007) provide a compatible example by estimating the economic impact of habitat enhancements for upland birds developed through government incentive programs to offset their implementation cost. In the case of corn, permanent herbaceous game bird habitat adjacent to fields (compared to forested field borders) also improved crop yields within the outer-most field rows. Such edge rows are normally considered to be less productive than field interiors due to soil compaction, shading by adjacent trees, competition from tree roots and other factors (Boatman and Sotherton, 1988; De Snoo, 1994), but here an enhanced yield was estimated at +$85.14/ha (Barbour et al., 2007). The parallel early successional habitat requirements of upland gamebirds and pollinators suggest scenarios in which pollinator habitat is targeted for enhancement would yield similar benefits.

Sandhu et al. (2008) used 'bottom-up' valuations of ecosystem services provided by organic farming compared to conventional farming in Canterbury, New Zealand, estimating and summing the separate value of a number of services. For example, pest control was valued using the avoidance cost of pesticides and pollination was valued as the savings in purchasing honey bee hives. However, it is often difficult to account for interactions between benefits in such models: avoiding the use of pesticides can benefit pollinators for example, therefore some of the costs saved from pesticide reduction, may also lead to savings in honey bee hives. Some authors have attempted to address these problems. For example, Raudsepp-Hearne et al. (2010) developed a valuation system based on 'bundles' of ecosystem services that often occur together. In this way, the interactions between services are captured and the double-counting problem of summing inventories of services is avoided. Alternatively, Farber et al. (2006) detail a framework in which the *changes* in ecosystem services occurring under different management strategies are valued using appropriate techniques (willingness to pay, market value, etc.), including non-monetary methods. The changes are then scored, weighted and summed to determine the most effective strategy overall.

These examples and the factors highlighted in Table 1 demonstrate that farming to improve ecosystem services is a delicate balance of trade-offs and requires a thorough understanding of the spatial and temporal dimensions of relevant services, whether they are targeted or are beneficial by-products. There are numerous tools in development to assist decision makers in weighing up ecosystem service options. In particular, the mapping of ecosystem service demands, supply and budgets (the net service demand or supply), is proving to be a useful conceptual method for understanding the ecosystem service provision and consumption in time and space, particularly as it allows the aggregation of many layers of information (Burkhard et al., 2009, 2012; van Wijnen et al., 2012). For example, mapping has been applied to the trade-offs between the soil erosion regulation and carbon sequestration of pine forests and their associated reduction in water yield in New Zealand on a national scale, where costs and benefits vary spatially (Dymond et al., 2012). Similarly, Kroll et al. (2012) applied a mapping approach to the trade-offs implicit in water, food and energy supply and demand along an urban–rural gradient, at three points in time since 1990, enabling the assessment of different regional land use changes on ecosystem service budgets. The development of such models at farm or landscape scales could assist in visualising net benefits of measures like pollinator habitat enhancement, and in providing landscape-specific management recommendations. This paper should facilitate greater awareness of some often overlooked non-target ecosystem services, which should be incorporated into such mapping endeavours in future work.

5. Conclusion

There is growing evidence that AES measures promoting pollinator habitat not only improve forage and nesting resources for bees but also contribute to the general protection of biodiversity, greater natural pest control, improved soil and water quality, and enhanced rural aesthetics. With these significant secondary benefits in mind, pollinator conservation can serve as a useful framework for achieving multiple objectives, and should be promoted as such. Benefits are particularly likely to occur at the landscape scale (Fiedler et al., 2008); as may be intuitively expected, the enhancement of ecosystem services can be more effective when adopted over wide areas rather than at only individual locations (Rundlof et al., 2008; Merckx et al., 2009). The responsibility underlying this opportunity requires that management strategies for implementing pollinator AES measures attempt to balance as many of these resource objectives as possible, and thus maximize possible ecological gains. Of course, the full potential of this AES framework will be realized only if additional policies are developed to address other factors associated with bee declines, such as pesticide use and the human-mediated movement of bee pathogens.

Conversely, opportunities are likely to exist to modify other existing AES practices to increase their benefit to pollinators. For example erosion control efforts using engineered vegetation could incorporate more wildflowers into their design, thus not only providing secondary benefits to pollinators, but also potentially enhancing beneficial insect populations, and overall biodiversity (including birds, mammals, etc.). However, there are many trade-offs to take into consideration when planning for this kind of multiple ecosystem service provision, Such a multi-factor approach to conservation would help to shift agriculture away from a crisis–response model and enhance the resistance and resilience of farm systems in the face of future ecological and economic challenges.

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