

Conservation ecology of bees: populations, species and communities*

Tomás E. MURRAY¹, Michael KUHLMANN², Simon G. POTTS³

¹ Crops Research Centre, Teagasc, Oak Park, Carlow, Co. Carlow, Ireland

² Department of Entomology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

³ Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Earley Gate, Reading RG6 6AR, UK

Received 30 October 2008 – Accepted 13 February 2009

Abstract – Recent concerns regarding the decline of plant and pollinator species, and the impact on ecosystem functioning, has focused attention on the local and global threats to bee diversity. As evidence for bee declines is now accumulating from over broad taxonomic and geographic scales, we review the role of ecology in bee conservation at the levels of species, populations and communities. Bee populations and communities are typified by considerable spatiotemporal variation; whereby autecological traits, population size and growth rate, and plant-pollinator network architecture all play a role in their vulnerability to extinction. As contemporary insect conservation management is broadly based on species- and habitat-targeted approaches, ecological data will be central to integrating management strategies into a broader, landscape scale of dynamic, interconnected habitats capable of delivering bee conservation in the context of global environmental change.

conservation / biodiversity / population / community / plant-pollinator

1. INTRODUCTION

Concerns about a potential pending global ‘pollinator crisis’ have been raised for over a decade, based on the evidence available at the time (Buchmann and Nabhan, 1996; Kearns et al., 1998; Kremen and Ricketts, 2000; Diaz et al., 2005), though such a crisis was questioned by Ghazoul (2005); but see Steffan-Dewenter et al., (2005). Prior to 2006, documentation of bee declines were limited to a few case studies and were generally taxonomically restricted and considered only specific locations (e.g. bumblebees, Peters, 1972, Williams P.H., 1986; honeybees, Williams I.H. et al., 1991; solitary bees, Westrich, 1989), and were not often published in mainstream scientific literature (e.g. Rasmont, 1988; Falk, 1991;

Banaszak, 1995). The need for more a comprehensive understanding of the global status and trends of pollinators triggered a number of projects and studies aiming to provide large-scale and taxonomically diverse assessments. In Europe, the ALARM project¹ provided the first national-scale assessments of shifts in whole bee communities in the UK and Holland (Biesmeijer et al., 2006) and demonstrated severe declines in bee diversity, abundance and ranges and also concurrent declines in bee-pollinated flowering plants. In North America, a synthesis of existing information was undertaken (National Research Council, 2006) and concluded that there were long-term declines in honeybees and some wild bees (most notably bumblebees). Recognition of widespread loss of pollinators and pollinator

Corresponding author: T.E. Murray,
tomas.murray@teagasc.ie

* Manuscript editor: Robert Paxton

¹ Assessing Large-scale Risks to biodiversity with tested Methods, www.alarmproject.net

services by the Convention on Biological Diversity (through the Agricultural Biodiversity programme and International Pollinator Initiative²) resulted in FAO coordinating the ‘Rapid Assessment of Pollinators’ status’ report (2008) which aims to compile global evidence of the extent of pollinator shifts and loss of pollination services. Together these sources, and many other studies (e.g. Klein et al., 2002; Larsen et al., 2005; Williams N.M. and Kremen, 2007), provide an overwhelming evidence-base for marked declines of many taxa of bees across the world.

The loss of bee species from communities may not be a random process e.g. large-bodied bees with higher pollination efficiencies can be more extinction prone (Larsen et al., 2005), and so has important implications for pollination services to crops and wild flowers (Memmott et al., 2004). Drivers of local bee extinctions can act differentially on particular bee traits such as size, foraging and nesting behaviour. For instance, in Californian agroecosystems, Larsen et al. (2005) reported that large-bodied bees were more extinction-prone, and Memmott et al. (2004) demonstrated that larger bees (such as bumblebees) tend to be more highly linked in plant-pollinator webs. Similarly wildfires were found to disassemble Swiss and Israeli bee communities in a non-random fashion, with extinction probabilities related to nesting guild, phenology, foraging behaviour and size (Potts et al., 2005; Moretti et al., 2009). However, the sensitivity of particular bee species to the wide range of natural and anthropogenic drivers remains largely unknown. It is therefore essential to understand the basic ecology of bees in order to predict how they respond to environmental change and how these changes can be mitigated against.

A general conceptual framework has been proposed to facilitate our understanding of how bees, and other “mobile-agent-based ecosystem service providers”, are affected by land-use change (Kremen et al., 2007). The model describes interactions between bees, the temporal and spatial availability of resources,

biotic and abiotic factors affecting bee fitness, the delivery of pollination services and how these are all potentially affected by land-use change, policy and market forces (Fig. 1). By adopting this model, i.e. incorporating individual behaviour, population biology and community dynamics, this review aims to highlight specific areas of bee ecology that will have the greatest impact on the development and application of conservation strategies.

2. AUTECOLOGY AND CONSERVATION

It is now widely accepted that sensible management begins with a sound, fundamental understanding of a species’ ecological interactions and natural history (Simberloff, 1988; Brussard, 1991; Schultz and Hammond, 2003). Nonetheless, detailed autecological study, like systematics, seems to lack the cachet of academic respectability that ensures practitioners of regular funding or even employment (Kim and Byrne, 2006). Unsurprisingly, we are woefully short on autecological information for rare and little-known species, but it is also true for many of the more charismatic bees, such as bumblebees (e.g. Kosior et al. 2007; Williams P.H. and Osborne, 2009).

These autecological data are of critical importance for calculating a suite of parameters which can be used to predict extinction risk as elements in population viability analysis (PVA) and identify traits correlated with vulnerability to extinction in phylogenetic comparative approaches (Schultz and Hammond, 2003; Fisher and Owens, 2004). Even basic ecological knowledge gleaned from the literature can be utilized to predict the risk of extinction and prioritise species of conservation concern. In the Lepidoptera, for example, traits associated with vulnerability to extinction, although frequently highly taxon dependent, typically include: dispersal ability, larval specificity, adult habitat breadth and length of flight period (Kotiaho et al., 2005).

It is important to note that autecological studies do not need to be mundane exercises in data gathering; rather, the autecological traits discussed below should be used to generate

² <http://www.cbd.int/programmes/areas/agro/pollinators.aspx>

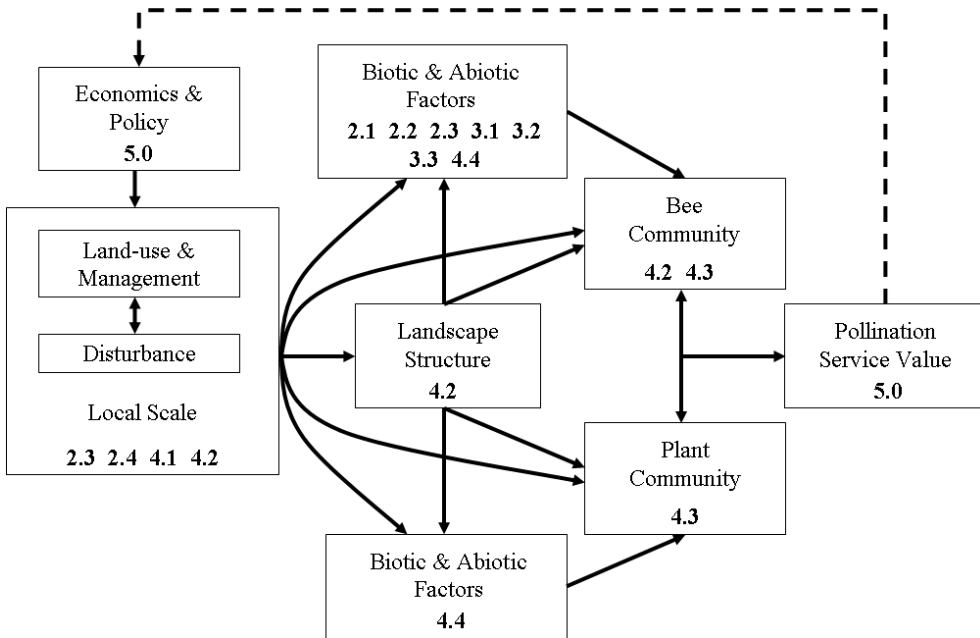


Figure 1. Conceptual framework for studying impacts of land-use change on bee conservation; incorporating the biology of the organisms involved, in addition to ecosystem service provision and its positive feedback into economics and conservation policy. Numbers in boxes refer to the relevant section in the text. Modified from Kremen et al. (2007).

testable hypotheses to drive several research projects. In the absence of detailed autecological information and long-term population data, we will continue to be forced to make several assumptions when both interpreting precipitous declines in numbers and when recommending appropriate management actions.

2.1. Socioecology

The primary effect of sociality on bee conservation biology is its impact on a species' population biology and genetics (reviewed in: Pamilo et al., 1997; Chapman and Bourke, 2001; Zayed, 2009). What best defines a population of bees is fundamentally tied to its level of social organisation and the resultant reproductive potential of each individual (Crozier and Pamilo, 1996). Thus, a population of a solitary species, where each individual may reproduce, would be a population of individuals; whereas a population of eusocial bees would be a population of

colonies, as within a colony one or few related queens reproduce and most individuals are non-reproductive workers. Consequently, the ratio of the effective to the census population size can rapidly decrease with increasing social organisation (Pamilo and Crozier, 1997; Chapman and Bourke, 2001). Similarly, the ease with which we can establish the population size, and therefore the conservation status, of a taxon typically decreases with increasing social complexity.

Although the majority of bees are solitary, all levels of social organisation occur within the Apoidea (Michener, 1974; Crozier and Pamilo, 1996). Some families of bees, the sweat bees (Halictidae) in particular, are noteworthy among insects due to their substantial interspecific (Danforth, 2002; Brady et al., 2006) and intraspecific (Soucy, 2002) variability in social behaviour. The behavioural plasticity observed within halictid social behaviour is of particular relevance as an example of how some species can exhibit more than one type of sociality across geographic and

climatic gradients e.g. both *Lasiglossum calceatum* and *Halictus rubicundus* are social in lower altitudes and solitary at higher altitudes (Sakagami and Munakata, 1972; Eickwort et al., 1996). In the absence of detailed autecological information for many rare species, utilising methods such as phylogenetic comparative approaches (e.g. Fisher and Owens, 2004) in well-described groups such as the sweat bees could highlight previously unreported socially polymorphic taxa in other families and stimulate further ecological research. For those species where sociality has been confirmed, establishing both the level and plasticity of social organisation is an important first step in any conservation programme. As mentioned, the effective population size, and therefore the vulnerability, of a species depends not only on the number of nests, but also on the mode of colony foundation, number of reproductive individuals and reproductive skew among these individuals (see Sect. 3.2 Mating systems).

2.2. Parasitism

An adjunct to the levels of social organisation found within bees are their varying forms of parasitism, namely: usurpation and robbing, social parasitism and cleptoparasitism (Michener, 2007). In all cases, the parasite benefits from the resources gathered and/or constructed by the host, with the host presumably incurring a fitness cost in the process. It is estimated that 15–20% of all bee species are parasites (Wcislo and Cane, 1996), with the percentage of parasitic species tending to increase with latitude (Wcislo, 1987; Petanidou et al., 1995). Despite the relative abundance and mostly temperate distribution of parasitic bees, relatively little is known about their biology as their population sizes rarely become large enough for detailed study (Scott et al., 2000; Bogusch et al., 2006).

The term ‘coextinction’ was coined after Stork and Lyal (1993) drew attention to the likelihood that many parasites may go extinct when their hosts go extinct. In a recent review, Koh et al. (2004) found that approximately 5000 insect species are likely to be en-

dangered as a direct consequence of the endangerment of their hosts and that at least 100 species of beetles, lice and butterflies have probably gone extinct in the last 200 years due to the extinction of their hosts. Although it is difficult to generalise about the pattern and degree of specialisation across parasitic bee taxa (e.g. Bogusch et al., 2006), most studies have revealed a strict concordance between physiology and behaviour of parasite and host (Wcislo, 1987; Scott et al., 2000). Therefore, determining the degree of specialisation becomes increasingly important as it is probably proportional to the probability of host and parasite becoming coextinct. Furthermore, due to their generally lower population sizes, declines in parasite populations may frequently precede those of their host populations, as observed by Rasmont et al. (2005) in Belgium where declines of megachilid and anthophorid cleptoparasites were found to be disproportionately higher than those of their hosts.

2.3. Floral resources and specialisation

Bees are herbivores that feed their larvae with a mixture of pollen and nectar or, rarely, plant oils (Michener, 2007). Robertson (1925) was one of the first to recognize that bees do not collect pollen on flowers randomly but that some species demonstrate floral specificity when harvesting pollen only on a limited number of plant taxa. He introduced the terms monolecty, oligolecty and polylecty to distinguish between pollen specialists and generalists, respectively. This classification inadequately reflects the complex relationships between bees and their pollen hosts and was updated by Cane and Sipes (2006), and recently modified by Müller and Kuhlmann (2008; Tab. I).

Even generalist bees show a restricted range of pollen sources (Westrich, 1989; Müller, 1996, Müller and Kuhlmann, 2008); pollen might not be an easy to use protein source. Praz et al. (2008) demonstrated that several specialized bee species fail to develop on non-host pollen, indicating that the pollen of some plant taxa, e.g. Asteraceae,

Table I. Classification of floral specificity of pollen collection by Robertson (1925), Cane and Sipes (2006), and an updated classification proposed by Müller and Kuhlmann (2008) (differences in terminology and definitions in *italics*).

Robertson (1925)	Cane and Sipes (2006)	Müller and Kuhlmann (2008)
Monolecty	Monolecty Pollen collection on only one plant species even in the presence of one or more sympatric species of the same genus	Monolecty Pollen collection on only one plant species even in the presence of one or more sympatric species of the same genus (<i>see also Narrow oligolecty</i>)
Oligolecty	Narrow oligolecty Pollen collection from two to several species belonging to one plant genus	Narrow oligolecty Pollen collection from two to several species belonging to one plant genus (<i>pollen collection on only one plant species in the absence of co-flowering congenics is referred to as a special case of narrow oligolecty</i>)
	Oligolecty Pollen collection from <i>two to several species belonging to one to four genera belonging to one family</i>	Broad oligolecty Pollen collection from <i>two to several genera belonging to one plant tribe, subfamily or family</i>
	Eclectic oligolecty Pollen collection from two to four plant genera belonging to two or three plant families	Eclectic oligolecty Pollen collection from two to four plant genera belonging to two or three plant families
Polylecty s.l.	Mesolecty Pollen collection from more than four plant genera belonging to two or three plant families <i>or big tribes</i>	Mesolecty Pollen collection from more than four plant genera belonging to two or three plant families
	Polylecty Pollen collection from various genera belonging to <i>four to <25% of available plant families</i>	Polylecty with strong preference <i>Pollen collection from several plant families, but one plant clade (family, subfamily, tribe, genus or species) predominates</i>
	Broad polylecty Pollen collection from various genera belonging to <i>>25% of available plant families</i>	Polylecty s.s. Pollen collection from various genera belonging to <i>at least four plant families</i>

possesses unfavourable or protective properties that render its digestion difficult. This suggests that the successful utilization of pollen by bees in general might require special physiological adaptations to cope with toxic secondary chemicals of their hosts. Selection should favour the evolution of such adap-

tations and eventual host specificity in bees (Praz et al., 2008) if they fit the physiological-efficiency hypothesis (Cornell and Hawkins, 2003), which predicts a physiological trade-off in the ability to efficiently utilize alternative hosts as a consequence of these adaptations (Singer, 2008).

The quantitative pollen requirements of bees are little known. In a study of 41 bee species Müller et al. (2006) revealed that 85% of them require the whole pollen content of more than 30 flowers to provision a brood cell and some species even needed the pollen of more than a thousand flowers to rear a single larva. In combination with the often restricted foraging range of small bees (see Sect. 3.1 Dispersal), this implies that tens of thousands of flowers of a certain plant must be available within range to sustain a viable population of an oligolectic bee species. Hence, the loss of plant diversity and flower quantity due to habitat destruction and fragmentation of the landscape is assumed to be responsible for the decline of many bee species (Müller et al., 2006). Social bee species are typically polylectic (Michener, 2007) and are generally believed to be less prone to local extinction. However, Kleijn and Raemakers (2008) have recently shown that bumblebee species whose populations are in decline use a narrower spectrum of host plants than bumblebees with stable populations.

Specialized bees generally do not switch to other host plants, even if their preferred plants are not in flower (Strickler, 1979; Williams N.M., 2003). Hence, selection for synchrony of bee emergence with host plant flowering that is positively affecting individual fitness (Powell and Mackie, 1966) can be expected, especially in arid and semi-arid environments with highly variable precipitation. Anecdotal observations and experimental data suggest that in arid environments rainfall triggers the emergence of oligolectic bees in particular (reviewed in Danforth, 1999). Evidence from western South Africa challenges this view (Mayer and Kuhlmann, 2004) and contradicts the assumption that bees react to the same environmental cues for emergence as their host plants for flowering e.g. rainfall (Linsley, 1958; Weislo and Cane, 1996; Tauber et al., 1998). However, generally it is hypothesized that host plant synchrony might be a mechanism for an elevated rate of speciation in desert bees (Minckley et al., 2000; Danforth et al., 2003) explaining the higher bee species diversity in semi-arid and arid environments. Thus, oligolectic bees that are strictly dependent on

their host plants are most species rich in desert and Mediterranean environments, and less diverse in temperate biota (Moldenke, 1979).

2.4. Nesting resources

Nesting resources for bees include the substrates within, or on which, they nest and also the materials required for nest construction. Bees are extremely diverse in their nesting ecology and comprise a number of distinct guilds (O'Toole and Raw, 1991): miners, carpenters, masons, social nesters and cuckoos. Mining bees include all Andrenidae, Melittidae, Oxaeidae, Fideliinae and most Halictidae, Colletidae and Anthophorini species. Miners excavate tunnels in the ground or soft rocky substrates and line their tunnels with glandular secretions. Carpenter bees also excavate nests, but use wood as a substrate, and include species in the genera *Xylocopa*, *Ceratina* (Apidae) and *Lithurgus* (Megachilidae). In contrast, mason bees (most Megachilidae) utilise pre-existing holes which can be in the form of hollow plant stems, abandoned insect nest burrows in the ground or woody substrates, small cavities or cracks in rocks and even snail shells. Masons then line the inside of the pre-existing hole with materials such as leaves or soil. Within the mason guild, the leaf-cutter bees use only freshly gathered leaf or petal material to line their nests and are members of the *Megachile* and *Creightonella* genera of the Megachilidae. Social nesters tend to use relatively large pre-existing cavities to establish social colonies and include three taxa within the Apidae: honeybees (*Apis*), bumblebees (*Bombus*) and stingless bees (*Meliponini*). One guild of bees, the cuckoo bees or cleptoparasites, are found in several families and do not construct their own nests but instead parasitize the nests of other bees by laying their eggs on larval provisions provided by the host.

Potts et al. (2005) demonstrated that the availability of both nesting substrates and construction materials were primary determinants of overall bee community composition. Furthermore, the dominant ecological perturbation, fire, resulted in a marked turnover of

nesting resources, resulting in large shifts in the relative proportions of nesting guilds. Other resources shown to affect bee nesting success include: the abundance, size and species of trees in tropical forests for stingless bees (Eltz et al., 2002; Samejima et al., 2004); cavity shape and size for honeybees (Schmidt and Thoenes, 1992; Oldroyd and Nanork, 2009), and the diameter of pre-existing holes for colletid bees (Scott, 1994); soil hardness, slope and aspect of the ground for halictid bees (Potts and Willmer, 1997); and soil texture for solitary bees (Cane, 1991).

The diversity of nesting strategies and the specialisation of guilds means that the availability of the correct quantity and quality of resources, both in space and time, are key determinants for which species a landscape can support (Tscharntke et al., 2005). Any environmental disturbance (e.g. habitat loss, fragmentation, agricultural intensification, or fire) will alter the distribution of nesting resources. As bees are central place foragers and have species-specific flight distances, the location of the nest determines what floral resources are potentially available. The nesting traits of bee species will therefore determine their sensitivity to environmental change (Moretti et al., 2009). In order to manage the landscape for bee conservation it is therefore essential to understand how land use change affects nesting resources and how this interacts with the availability of other resources such as nectar and pollen.

3. POPULATION BIOLOGY AND CONSERVATION

Species are driven to extinction by both human-mediated deterministic factors and stochastic factors (Frankham et al., 2002). In general, a species' population size is initially reduced by deterministic factors such as habitat loss, fragmentation, overexploitation, introduced species, pollution and climate change. Populations may then further decline to a point of 'no return' where demographic, environmental and genetic stochasticity and catastrophes eventually drive them to extinction. Consequently, as both absolute population size

and spatio-temporal variability in population size are universally the most important predictors determining extinction risk, their accurate estimation is of paramount importance to conservation biology (Frankham et al., 2002; O'Grady et al., 2004).

Insect populations commonly experience large annual fluctuations in population size, arising from natural variation in population growth and measurement errors in population estimates (e.g. Schultz and Hammond, 2003). Unfortunately, bee populations and communities are no exception, displaying considerable spatio-temporal variation in abundance and composition (Williams N.M. et al., 2001; Roubik, 2001; Eltz, 2004; Tylianakis et al., 2005; Petanidou et al., 2008). The highly variable nature of these ecological data complicates the determination of the conservation status of a species, as devastating declines may occur, but remain undetected until a sufficient period of time has elapsed after monitoring the population. Unfortunately, this typically leaves managers and policy makers in a reactive posture as the decline might be demonstrated, but only after it has already seriously weakened the population.

Although in many cases an experimental approach may be more appropriate, in practice, especially for rare species, the logistics, lack of replication and spatial scales involved have driven the proliferation of modelling approaches to test hypotheses about the causes of decline and the response of populations to management practices or future changes in the environment (e.g. risk-based viable population monitoring, Staples et al., 2005). In a review of the ecological tools available to conservationists to intervene in the extinction process, or even predict precipitous declines, Norris (2004) outlines a 'toolbox' for the management of threatened species: statistical models of habitat use, demographic models and behaviour-based models. In particular, population viability analysis (PVA) is one of the most widely applied demographic models in conservation (Lande et al., 2003), and as recent modifications to PVA now allow for less intensive data (e.g. shorter time series and population surveys) more often available for insect populations, it has been successfully

applied to endangered insects, particularly butterflies (e.g. Schultz and Hammond, 2003; Schtickzelle and Baguette, 2004).

There are innumerable parameters that may be discussed in relation to studying the population biology of a single species. Below we highlight three key areas of study that can significantly influence the estimation of population size, growth rate and persistence of bee populations.

3.1. Dispersal

Female bees forage from a single location, their nest, and as such are central place foragers (Schoener, 1979). Theoretical studies frequently emphasise the role of dispersal ability and emigration between patches in predictions of minimum viable population size (Hanski and Pöyry, 2006), thus information of their flight range is vital for bee conservation to make sure their habitat requirements are met within their range of activity (Westrich, 1996; Cresswell et al., 2000). Known foraging distances of bees range from 0.1 km to a maximum of 45.5 km in *Eufriesea surinamensis*, with values for most species below 1 km (summarized in Greenleaf et al., 2007) and a strong correlation exists between the intertegular span (ITS) and foraging range that can be used as a valuable tool to predict foraging ranges based on a simple measurement of ITS. In addition, knowledge about the foraging range is also important for estimation of area requirements of bees for providing optimal pollination service in agriculture (Kremen et al., 2004). For conservation measures it is vital to take into account that species with a small foraging range require more diverse resources per unit area than species with similar needs but greater range (Cresswell et al., 2000). Thus, for many species local habitat structure appears to be more important than large-scale landscape composition (Gathmann and Tscharrntke, 2002).

However, considering the abundance of data on the relationship between body size and foraging distance (e.g. Greenleaf et al., 2007), little data exist on how species' foraging ranges relate to male- or female-mediated

gene flow between populations. In the *Euglossini*, long-distance gene flow across the Andes was related to body size, with larger body sizes potentially conferring a dispersal advantage in terms of thermal tolerance and energy reserves for long-distance dispersal (Dick et al., 2004). In contrast, the level of population genetic subdivision (e.g. F_{st}) within the honeybee *Apis mellifera* was almost twice as high in South Africa (0.105) compared to Germany (0.064), despite the fact that the sampled subpopulations in South Africa were geographically closer together (Moritz et al., 2007). Generalisations regarding gene flow and body size may be spurious, as a species' dispersal ability may equally be determined by a range of other socio-ecological factors, such as nest-site philopatry, lecty and tolerance to inbreeding depression (Packer and Owen, 2001; Packer et al., 2005). Resolving the determinants of gene flow between populations is of critical importance to all species-based conservation programmes and should be a fruitful avenue for future research in bee conservation.

Regardless of the lack of data regarding gene flow, population viability and minimum habitat requirements of bees (e.g. Larsen et al., 2005), small and isolated bee populations can persist for relatively long periods of time provided that the habitat remains unchanged (Kratochwil and Klatt, 1989). Basically bees are physiologically highly capable of flying long distances increasing the likelihood that a habitat is (re)colonized. Solitary bees have been found on lightships in the North Sea and Baltic Sea up to 10 km off the coast, bumblebees even up to 30 km distance from the nearest land, but most of the specimens were close to the end of their reproductive phase and thus not of significance for colonization (Haeseler, 1974). Capacity for (re)colonization is correlated to distance and habitat fragmentation (Steffan-Dewenter and Tscharrntke, 1999; Steffan-Dewenter and Westphal, 2008) but even areas neighbouring ancient suitable bee habitats are slowly recolonized (Forup et al., 2008) and isolated habitats like islands (Haeseler, 1976, 1978) are hardly reached by most bee species, limiting the potential success of ecological restoration measures

(Kuhlmann, 2000; Franzén et al., 2009). Despite the fact that the colonization ability of bees seems to be generally low, massive and short-term range extensions are known from a few species like *Andrena fulva* and *Bombus hypnorum* in NW Germany about a century ago (Wagner, 1938) and, more recently, *Andrena cineraria* (Haeseler, 1973), *Halicictus scabiosae* (Frommer and Flügel, 2005) and *Colletes hederæ* (Kuhlmann et al., 2007; Frommer, 2008).

3.2. Mating systems

In the context of population biology, the effective population size, population growth rate and variance in population growth rate of a species depend not only on the number of individuals and nests, but also on the level polygamy and inbreeding present within the population (Pamilo and Crozier, 1997; Chapman and Bourke, 2001). Due to the haplodiploid nature of bees, the effect of inbreeding on effective population size is a function of the sex ratio and level of polygamy (see Zayed, 2009). Briefly, as females are diploid, they contribute twice the genetic diversity to a population than haploid males, thus multiple mating by females increases the effective population size, but multiple mating by males decreases it, as several females in a population would carry the sperm of a single male (Crozier and Pamilo, 1996; Hedrick and Parker, 1997).

The majority of the 20–30 000 estimated bee species are solitary (Michener, 2007), yet knowledge of solitary bee mating systems is still quite limited compared to social species; the assumption that females of most species are monogamous remains (Eickwort and Ginsberg, 1980). Currently, there is insufficient genetic pedigree (genetic analysis of mother and offspring) data or behavioural observations to support this assumption (Paxton, 2005). For example, Blanchetot's (1992) genetic pedigree study of the solitary leafcutter bee *Megachile rotundata* supports monoandry in this bee, whereas in the primitively eusocial sweat bee *Lasiglossum malachurum* both field observations (Knerer, 1992) and genetic pedigree data (Paxton et al., 2002) indicate that

polyandry is common in this species. More data on other solitary and primitively social species are necessary before any generalisations over female mating systems can be made.

In contrast, better data on female mating systems exist for the eusocial bumblebees, honeybees and stingless bees. Single mating by females appears to be the norm for most bumblebees (Schmid-Hempel and Schmid-Hempel, 2000), but there are exceptions (*Bombus hypnorum*; Paxton et al., 2001). Honeybees are highly polyandrous (Schlüns et al., 2005), whereas stingless bees are typically monoandrous (Paxton et al., 1999; Peters et al., 1999). Given this disparity in female mating frequency, it is notable that both honeybees and stingless bees are exceptional in that males only mate once (Roubik, 1989; Koeniger, 1991); whereas, for most species, males probably mate repeatedly (Paxton, 2005).

Despite difficulties in systematically recording mating behaviour, there is a clear need to confirm where, when and how often mating occurs, especially as the reproductive rates of solitary bees can be surprisingly low (Minckley et al., 1994). Furthermore, the presence of distinct intraspecific variability in male mating behaviour, associated with (e.g. *Amegilla dawsoni*, Alcock, 1997) or without (e.g. *Andrena aglissima*, Paxton et al., 1999) size differences, represents a unique opportunity to further advance our understanding of how mating behaviour can influence reproductive success at a population level, and how this influences our estimation of population size and growth rate for conservation.

3.3. Predators, parasites and pathogens

Major factors limiting bee populations such as nest site or nest material (e.g. Potts and Willmer, 1997), climatic conditions (e.g. Pekkarinen, 1997) and pollen availability (e.g. Minckley et al., 1994) have received relatively detailed study compared to how predators, parasites and pathogens affect bee mortality, population dynamics and community composition. The potential for parasites and pathogens to limit, or regulate, bee populations is now glaringly apparent considering that

Varroa destructor parasitic mites, for example, destroyed 25–80% of managed honeybee colonies, and nearly all feral colonies, in parts of the United States during the mid-1990s (Sammataro et al., 2000). The epidemic of ‘Colony Collapse Disorder’ destroyed 50–90% of US colonies in affected apiaries in 2006/07, and also has been suggested to involve a contagious pathogen (Cox-Foster et al., 2007). It is possible that such marked declines may also occur in many populations of non-managed bees over similar geographic scales (e.g. *Andrena scotica*; Paxton et al., 1997), but such declines are frequently unrecorded or may be obscured by the considerable spatiotemporal variation in abundance observed in many species (Williams N.M. et al., 2001; Roubik, 2001; Tyljanakis et al., 2005). Furthermore, even sub-lethal effects of infection may alter plant-pollinator interactions and, therefore, ecosystem functioning (Eviner and Likens, 2008). For example, the ability of *Bombus terrestris* foragers to discriminate rewarding flowers based on either colour or odour decreased after being infected by the protozoan parasite *Crithidia bombi* (Gegeer et al., 2006).

Better data on the potential of parasites and pathogens to affect ecological interactions between species are available for the eusocial bumblebees. At the regional scale (50 km²), parasite diversity is proportional to regional bumblebee host distribution and local abundance; parasite load (the average number of parasite species per individual worker) is inversely proportional to host species diversity (Durrer and Schmid-Hempel, 1995; Schmid-Hempel, 2001). These data support the hypothesis that widely distributed (common) host species may be adapted to a wider variety of parasites, pathogens or strains of both, whereas locally occurring (rare) host species may be adapted to a subset of the parasites present (Price et al., 1986, 1988). When both rare and common host species coexist, the common species is expected to have a competitive advantage due to both its adaptation to a wider variety of parasites, and by maintaining a greater diversity of potentially more virulent parasites within regions. However, aside from cases of pathogen spillover from

introduced species (see Stout and Morales, 2009); there is currently little evidence regarding the role of parasites and pathogens as drivers of decline in bumblebees (Goulson, 2003; Williams P.H. and Osborne, 2009). Using a novel comparative approach to investigate the role of pathogens in eusocial lineages, Boomsma et al. (2005) propose a series of testable hypotheses regarding eusocial bee pathogens in comparison to eusocial wasps, ants and termites: orally transmitted diseases should be more common, more virulent and endemic than those found in ants and termites; the incidence of macroparasites (e.g. mites, nematodes, parasitoids) should be intermediate between wasps and termites; and vertical transmission of parasites should be more common in bees and wasps, particularly in colonies with multiple queens.

Other than phenomenological reports, little data exist on the impact of parasites or pathogens on the population dynamics in solitary bees. For example, the Stylopidae have the highest diversity of any strepsipteran family (ca. 160 species) and are exclusive endoparasites of bees (Pohl and Beutel, 2008), yet aside from their ability to effectively neuter their host (Wülker, 1964; Askew, 1971), relatively little is known about their impact on host populations (Kathirithamby, 1989). In the context of social evolution, predators, particularly ants, cause significant levels of mortality in solitary versus social ground-nesting bees and are, therefore, constraints on independent nesting. Over a five-week period, all nests containing only one female of the facultatively social halictid bee *Megalopta genalis* failed to survive brood predation by ants, whereas nests containing multiple females all survived (Smith et al., 2007). Similarly, Zammit et al. (2008) recorded colony survival and brood production rates in predator-excluded versus control nests of the cooperatively nesting allopapine bee *Exoneura nigrescens*: 77.8% of nests protected from ants survived, with an average 3.55 brood per nest, compared to 41% survival and 1.56 brood per nest in unprotected nests. Likewise, for eusocial bees, high predation rates have been recorded by predators such as the bee wolf, *Philanthus* spp.; typically-sized aggregations of these

crabronid wasps have been estimated to consume 1015 bumblebees per hour (Dukas, 2005) and around 30 000 honeybees per day (Simonthomas and Simonthomas, 1980). It is, therefore, unsurprising that in a recent meta-analysis on the impact of predation on ecosystem functioning, Knight et al. (2006) found that predators had a substantial negative impact on pollinator visitation rate and reproductive success of plants. However, the relative importance of top-down (predators, parasites and pathogens) *versus* bottom-up factors (floral and nesting resources) in regulating bee populations is still largely unknown.

4. COMMUNITY ECOLOGY AND CONSERVATION

The response of individuals, populations and communities of bees to changes in land-use is primarily driven by the spatial and temporal distribution of floral, nesting and overwintering resources in relation to the foraging and dispersal abilities of bees (Kearns et al., 1998; Kremen et al., 2007). Using concepts from network theory, recent advances in the study of plant-pollinator networks have considerably improved our ability to define and predict interactions between species at a community level and how the number, strength and symmetry of these interactions influence community tolerance to extinction (Memmott et al., 2004; Larsen et al., 2005; Bascompte and Jordano, 2007), especially in the context of global environmental change (Tylianakis et al., 2008).

4.1. Local scale: availability of critical resources

At the individual site or local scale, management and land-use practices determine the community composition of both pollinators and plants, and the extent to which biotic and abiotic factors affect both groups (Kremen et al., 2007; Fig. 1). Whether clumped in discreet patches or dispersed throughout the landscape, the distribution of floral and nesting resources largely dictates the structure and composition of bee communities. In relation to floral resources, including oils and resins, bees

are obligate pollen-foragers and generally both bee and flower abundance and species richness are positively associated (Wcislo and Cane, 1996; Steffan-Dewenter and Tscharnke, 2001; Potts et al., 2003; Holzschuh et al., 2007). For example, flower species richness, nectar resource diversity and nectar energy content explained 23% of the variation in bee community structure across six distinct Mediterranean habitats (Potts et al., 2006). Ultimately, increasing floral diversity provides a wider array of foraging niches for different functional groups of flower visitors (Fenster et al., 2004). Agri-environment schemes that alter the spatial and temporal distribution of floral resources frequently have the greatest impact on pollinator community composition. For example, in a study of 42 wheat fields in Germany, organic fields had over twice the species richness and twenty times the percentage cover of flowering plants compared to conventional fields, resulting in three times the species richness and almost eight times the abundance of bees in organic *versus* conventional fields (Holzschuh et al., 2007).

The availability of nesting resources also plays a key role in structuring bee communities (Cane, 1991; Eltz et al., 2002; Potts et al., 2005). In parallel with floral resources, the temporal and spatial distribution of nesting resources may determine the bee community composition in a given location. Eltz et al. (2002) found that the abundance, size and species of trees in tropical forests of Southeast Asia influenced the density of stingless bee nests. Similarly, in a hyperdiverse Mediterranean bee assemblage, the amount of exposed soil, the number of sloped surfaces and the number of cavities available as nest sites accounted for 26% of the variation in community composition (Potts et al., 2005). However, compared to floral resource use, relatively few data exist on the nesting requirements for many species. This may be due to the variety and often cryptic nature of bee nesting habits, ranging from burrows in the soil, in small pre-existing cavities in wood or stone, to nests constructed of excreted wax in larger cavities found in trees, rocks or rodent nests (see Sect. 2.4). Further studies are needed to assess whether nest sites are limiting resources

and what factors within a bee's flight range determine nest site selection.

In addition, indiscriminate use of pesticides and herbicides can both increase mortality rates (Johansen, 1977) and considerably reduce the availability flowering plants in agricultural areas (Firbank et al., 2003; Morandin and Winston, 2005). However, the intensity of pesticide and herbicide use is often associated with increased agricultural intensification and subsequent decline in floral and nesting resources (Kremen et al., 2002; Schweiger et al., 2005; Williams N.M. and Kremen, 2007). Therefore, separating the relative effects of each factor on bee community composition will improve future decisions about effective management of pollinators in agricultural habitats.

4.2. Landscape scale: habitat loss, fragmentation and land-use

Native habitat loss and fragmentation resulting from human activity are two of the primary factors driving declines of native species worldwide (Pimm et al., 2001). The synergistic effect of loss and fragmentation reduces gene flow and recolonisation between patches, lowering persistence of both subpopulations and networks of meta-populations (Hanski, 1998). Currently, there is no consensus on how bee communities respond to habitat fragmentation as empirical studies reveal a range of responses to fragment size, from positive (Cane and Tepedino, 2001; Donaldson et al., 2002) to negative (Steffan-Dewenter et al., 2002; Klein et al., 2003; Ricketts, 2004; Tab. II). This variability parallels that found in other animal groups (e.g. Vandergast and Gillespe, 2004) and indicates that responses may differ depending on life history and other species-specific attributes, such as dispersal ability and floral specificity (Cane and Tepedino, 2001; Zayed et al., 2005). A further complication occurs when the response of a taxon is obscured by the composition of the surrounding matrix of habitats and its influence on the availability of floral and nesting resources (Eltz et al., 2002; Cane et al., 2006; Williams N.M. and Kremen, 2007). Therefore, our limited knowledge of dispersal (see Sect. 3.1) and popula-

tion structure (see Zayed, 2009) prevent reliable estimation of the carrying capacity of different habitats and habitat mosaics, further complicating the assessment of their conservation value.

Globally, conversion of native habitats to agriculture is the primary form of land-use change and the largest cause of native habitat loss and fragmentation (Tilman et al., 2001; DeFries et al., 2004). The dominance of agro-ecosystems worldwide means that increasingly bee populations exist at the interface of agricultural and natural habitats or within agricultural areas. Although mass-flowering crops can be beneficial in some cases (e.g. Westphal et al., 2003, 2009), declines in both bee abundance and species richness with increasing agricultural intensity have been reported from a wide variety of agro-ecosystems (Steffen-Dewenter and Tscharnkte, 1999; Kremen et al., 2002; Ricketts, 2004; Chacoff and Aizen, 2006). Generally, agro-ecosystems that contain a mosaic of semi-natural habitats throughout the landscape can maintain significant levels of bee diversity and abundance (Tscharnkte et al., 2005; Winfree et al., 2007), even at regional scales (Tylianakis et al., 2005). Results from the recently completed European Union Greenveins project demonstrated that, for temperate European agro-ecosystems, once regional effects (i.e. country) were removed, variables describing land-use intensity and the spatial distribution of semi-natural habitats at the landscape scale (4 km²) were superior to local scale variables (0.008 km²) in explaining bee community composition (Schweiger et al., 2005). In a separate analyses of the same data, Hendrickx et al. (2007) affirm that land-use intensity and proximity to semi-natural habitats best explained bee species richness across landscapes, but loss of bee species richness was not solely the result of declines within habitats, but was also due to increased homogenization of community composition between habitats.

4.3. Plant-pollination networks

As there is a distinct lack of data on how pollinator communities disassemble;

Table II. Attributes of habitat fragmentation studies for native bee communities. Modified from Cane (2001).

Country	Habitat	Cause of fragmentation	Parameter	No. of sites	No. of bee taxa	Abundance of non- <i>Apis</i> bees	Trend	Ref.
Argentina	Dry thorn scrub	Agricultural clearing	Fragment size	8	43	481	Species richness declined with decreasing fragment size.	Aizen and Feinsinger (1994)
Brazil	Rainforest	Experimental deforestation	Fragment size	4	16	1092	Abundance decreased with fragment size.	Powell and Becker et al. (1980)
Brazil	Rainforest	Experimental deforestation	Fragment size	7	16	290	Abundance increased with fragment size.	Becker et al. (1991)
Brazil	Atlantic forest	Agricultural clearing	Fragment size and level of disturbance	9	21	3653	No effect of fragmentation due to high variability of species composition and abundance between sites.	Tonhasca et al. (2002)
Costa Rica	Agricultural (coffee)	Agricultural clearing	Distance to forest patch	16	40	618	Species richness was significantly higher in farms within 100 m from forest patches.	Ricketts (2004)
Costa Rica	Tropical forest	Agricultural clearing	Fragment size, shape, isolation and context	22	117	1537	Fragment size, shape, isolation and context affected community composition, but not abundance or species richness.	Brosi et al. (2008)
Europe (7)*	Agricultural (various)	Agricultural clearing	Land-use intensity; habitat diversity; distance to semi-natural habitat	24	115	> 14529 **	Across landscapes, bee species richness increased with habitat diversity and proximity of semi-natural habitat, but decreased with increasing land-use intensity.	Hendrickx et al. (2007)
Germany	Agricultural (cereals)	Agricultural clearing	Distance to semi-natural grassland	40†	23	212	Species richness and abundance decrease with increasing isolation.	Steffan-Dewenter and Tschamtké (1999)
Germany	Agricultural (cereals)	Agricultural clearing	% semi-natural grasslands within 3 km	15	36	1340	Abundance and diversity of solitary bees were correlated with % semi-natural areas up to 750 m, no effect found for <i>Bombus</i> or <i>Apis</i> .	Steffan-Dewenter et al. (2002)

Table II. Continued.

Country	Habitat	Cause of fragmentation	Parameter	No. of sites	No. of bee taxa	Abundance of non- <i>Apis</i> bees	Trend	Ref.
Indonesia	Rainforest	Agricultural clearing	Land-use intensity	12	22	401	Solitary bee abundance, not species richness, increased; social bee abundance and species richness decreased.	Klein et al. (2002)
Indonesia	Agricultural (coffee)	Agricultural clearing	Amount of shade, distance to forest patch	24	29	> 895 †	Solitary bee diversity increased with less shade; social bee diversity decreased with distance to forest patch.	Klein et al. (2003)
South Africa	Renosterveld shrubland	Agricultural clearing	Fragment size	24	19	-	Vegetation cover had a greater effect than fragment size on bee species richness and composition.	Donaldson et al. (2002)
U.S.A.	Scrub desert	Urbanisation	Fragment size and age	59	62	2512	Species richness decreases with smaller fragment size. Fragment size and age had greatest effect on ground-nesting specialists.	Cane et al. (2006)
U.S.A.	Agricultural (sunflower)	Agricultural clearing	% of semi-natural habitat within 3 km	16	33	5732	Species richness and abundance increased with increasing % semi-natural habitat.	Greenleaf and Kremen (2006)
U.S.A.	Various	Agricultural clearing, urbanisation	% of forest habitat within 1.6 km	40	130	2551	Species richness and abundance decreased with increasing forest cover, but increased with agriculture and urbanisation.	Winfree et al. (2007)
U.S.A.	Agricultural (tomato, melon, pepper)	Agricultural clearing	% of forest habitat within 0.5–3 km	29	54	4592	No effect of % of forest habitat and species richness on crops.	Winfree et al. (2008)

* Belgium, Czech Republic, Estonia, France, Germany, Netherlands, Switzerland.

** The number of non-*Apis* bees was not indicated; therefore bees of 8.5–12 mm in length identified by Schweiger et al. (2005) were excluded.

† 40 habitat 'islands' consisting of 4 mustard and 4 radish plants.

‡ The number of non-*Apis* eusocial bees was not indicated.

predictions arising from the recent proliferation of simulation studies based on networks of plant-pollinator interactions may be a valuable source of testable hypotheses (reviewed in Bascompte and Jordano, 2007). At the community level, interactions between species are the “glue of biodiversity” (Thompson, 2005) and mutualistic networks provide well-defined and predictable patterns of interdependence between species. Specifically, plant-pollinator networks can be described by two properties: they are very heterogeneous, with a few species much more connected than by chance; and they are highly nested, whereby specialists interact with distinct subsets of the species interacting with generalists (Bascompte and Jordano, 2007). As a result of this asymmetry in specialisation, plant-pollinator networks are reciprocally redundant and predicted to be relatively tolerant to extinction, as only the minority of plant species are likely to lose all their pollinator species as pollinator communities disassemble (Memmott et al., 2004). Notably, community resilience in plant-pollinator networks is predicted to be enhanced by increased species diversity and the number of species interactions (Okuyama and Holland, 2008). Furthermore, understanding the nested structure of plant-pollinator networks can explain why the reproductive output of both specialist and generalist plant species is similarly affected by habitat fragmentation (Ashworth et al., 2004); how invasive species rapidly become integrated into existing plant-pollinator networks (Memmott and Waser, 2002; see Stout and Morales, 2009); the rate of community disassembly with habitat loss (Fortuna and Bascompte, 2006); and how the structure of plant-pollinator networks remain largely stable, despite considerable temporal variation in the number, strength and symmetry of plant-pollinator interactions (Petanidou et al., 2008).

Currently, the only empirical study of bee community disassembly and its effect on pollination is that of Larsen et al. (2005). Using wild bee data from Kremen et al. (2002), the study found that the relationship between species richness and pollination is approximately concave up, indicating that the first species extinction could lead to rapid reduction in pollination. Two main factors corre-

lated with the loss of pollination function in bee communities: the non-random loss of species and the absence of strong density dependence following species loss. Bee species did not disappear randomly from sites; instead species were lost in an ordered fashion, with the largest, more efficient pollinators more likely to experience local extinction. Accordingly, 86% of sites experienced a greater loss of pollination function than would be expected by random species loss. This study affirms the sentiment expressed by Memmott et al. (2004), that plant-pollinator networks may be tolerant, but not immune, to extinction. Clearly, there is a dire need for empirical data regarding critical thresholds of species extinction and collapse of plant-pollination networks (Fortuna and Bascompte, 2006).

4.4. Climate change

Thomas et al. (2004) predicted that by 2050 climate change, even in the absence of other drivers of extinction, would doom 15–37% of all species to eventual extinction. The prediction is based on the application of an established ecological pattern, the species-area relationship, to data on the current distributions and climatic envelopes of 1103 species. Although their approach has been heavily criticised (e.g. Lewis, 2006), the study did raise critical questions regarding the response of species to climate change, such as: how many species have distributions primarily governed by climate; and to what extent do current distributions truly reflect limits of climate tolerances?

Although the uncertainty in their models preclude any firm generalisation, Dormann et al. (2008) found that climate accounted for 64.1% of the variation in the pattern of species richness at the landscape scale for wild bees in temperate Europe, compared to landscape structure (27.7%), soil (7.1%) and land-use intensity (1.2%). Furthermore, in a recent study simulating phenological shifts with a real community of plants and pollinators, Memmott et al. (2007) estimate that, over the past 100 years, global warming has advanced the first flowering date of plants and the seasonal flight activity of some pollinating insects

(mostly butterflies) by, on average, 4 days per degree C in temperate zones, resulting in between 17–50% of all pollinator species experiencing a disruption in food supply.

Broad trends regarding the impact of climate change on plant-pollinator networks are emerging (Tylianakis et al., 2008), but as any alteration in climate will be superimposed upon other, multiple interacting drivers of global change, significant challenges in predicting future responses remain.

5. HOW ECOLOGY INFORMS BEE CONSERVATION STRATEGIES

Knowledge of the basic ecology of bees is essential for underpinning the development and implementation of conservation strategies (Byrne and Fitzpatrick, 2009). Understanding the factors that regulate bee populations and communities, and the sensitivity of bee traits to these factors, allows specific management options to be identified for individual species and entire assemblages. A first step is to identify the resource requirements of the target bee taxa to ensure that the appropriate quantity and quality of these are provided spatially and temporally. These include both forage (pollen, nectar) and nesting (substrates and construction materials) resources and the provision of suitable abiotic conditions (microclimate and local topography). The distribution of resources must fall within the forage and/or dispersal ranges of the bee species considered, as different parts of the landscape often provide complementary resources, leading to the concept of partial habitats (Westrich, 1989). Assessing the resource distributions within the landscape may reveal that a single limiting resource is missing which can then be supplemented through management practices (e.g. provision of flower-rich field margins) to support bee conservation (see below).

A supply of optimal resources is not enough on its own; it is also important to understand how bees respond to landscape-scale changes in their environment. The geographic scale over which negative pressures affect bees, coupled with individual species' ability to disperse throughout the landscape, will determine whether bees can avoid irreversible popula-

tion decline. For instance, habitat loss and fragmentation can result in resource depletion, and thresholds for foraging and nesting resources will determine the carrying capacity of remaining habitats. Habitat area is known to impact on bee community composition (Steffan-Dewenter, 2003) and minimum patch sizes are important for the persistence of these communities (Hanski and Pöyry, 2006; Kremen et al., 2004). The configuration of the landscape, and how bees are able to disperse through the landscape, will determine whether spatially fragmented resources are available (Steffan-Dewenter and Tschardt, 2002; Tschardt and Brandl, 2004). The protection of key habitats and connectivity within the landscape (Gilbert et al., 1998; Tewksbury et al., 2002) therefore represents an important tool for bee conservation (see below). Other pressures such as grazing (Vulliamy et al., 2006) and fire (Potts et al., 2003) modulate the availability of resources in the landscape and managing grazing regimes and burning practices can fundamentally alter habitat quality for bees. Daily activity patterns and seasonal phenology may also determine the level of risk of bee exposure to pesticides and other agrochemicals (Brittain et al., unpubl. data). Altering the timing of pesticide application from midday to early morning or late evening can ensure that the window of maximum toxicity does not overlap with the times when bees are foraging on crops (Kevan, 1975). Similarly, modifying the types and application regime of herbicides can facilitate the maintenance of diverse flower communities within intensive agro-ecosystems (Westbury et al., 2008).

There are two broad and complementary categories of bee conservation approaches, both of which can be more effective when informed by bee ecology: species-targeted approaches and habitat-targeted approaches. Species-targeted approaches focus on individual species, or broader taxa, and often provide some kind of legal protection which aims to prevent activities causing direct mortality to individuals (including collection) (see Byrne and Fitzpatrick, 2009). One example is the Biodiversity Action Plan (BAP) in the UK which includes 17 species of bees (www.ukbap.org.uk). BAP is the UK Government's

response to the Convention on Biological Diversity and is a detailed plan for the protection of the UK's biological resources. Each UK BAP priority species action plan has an overview of the status of a species, information on the threats facing it, actions to achieve the action plan, and broad policies developed to conserve it. The core of the bee BAPs is based on detailed autecology of the target species or, if this is not available, then this is an initial priority step in developing a conservation plan. Another form of species protection is the IUCN Red Lists which include bees in several countries (e.g. Finland, Germany, Hungary, Ireland, Netherlands, Slovenia, Sweden, Switzerland and UK; see Byrne and Fitzpatrick, 2009). These priority species lists can clearly direct prioritization of conservation actions at national levels, but action should not be exclusive to listed species (Fitzpatrick et al., 2007).

Complementing the species-targeted actions are habitat-based approaches which focus on conserving and restoring important bee habitats. In some cases these will be specifically for bees, but in many cases they are aimed at enhancing wider biodiversity, which may also include bees. Many national protected areas and networks are natural or seminatural areas designated on the basis of priority habitats (e.g. Special Areas of Conservation in Europe, EC Habitats Directive 92/43/EEC) which in many terrestrial systems often include diverse floral resources which can support bees. In addition to protected areas, more ubiquitous habitats can be managed for conservation purposes. The UK BAP, for instance, includes a number of Habitat Action Plans which have detailed actions and targets for conserving these habitats; important bee habitats included are calcareous grasslands, hedgerows, and heathlands. In addition to natural areas, agro-ecosystems can be effectively managed for bees by exploiting the known ecological requirements of bee taxa. Agri-environment schemes aim to enhance general farmland biodiversity and in the UK include several bee-specific options. The English Entry Level Stewardship (Defra, 2005) financially supports farmers to manage their farms in a way which enhances the resources avail-

able for bees, for instance option EF4 involves sowing fields with pollen and nectar flower mixes. The options developed in this agri-environment scheme, and others in Europe and elsewhere, were mostly founded upon rigorous scientific work on bee ecology to identify the specific floral resource requirements for bees in both arable (Meek et al., 2002) and intensive grassland systems (Potts et al., in press).

6. CONCLUSIONS

Combinations of protected area networks and bee-friendly habitats within agriculture will become increasingly important for bee conservation as the impacts of global environmental change manifest themselves (Tylianakis et al., 2008). Currently, high quality habitats for bees may become unavailable as bee climatic envelopes shift and/or habitats become degraded. By taking a wider landscape approach and linking up fragments of (semi-) natural landscape with linear features, such as hedgerows and field margins, it will be possible to increase landscape connectivity and allow bees to forage and disperse to more suitable areas under global change (Gilbert et al., 1998; Tewksbury et al., 2002). Indeed, understanding the traits influencing the sensitivity of bees to climate change is essential if we are to manage our bee communities in the future.

ACKNOWLEDGEMENTS

The authors would like to thank L. Nilsson, T. Eltz and R. Paxton for insightful comments that improved the manuscript, and the editors for the invitation to contribute to this special issue.

Écologie de la conservation des abeilles : populations, espèces et communautés.

Apoidea / biodiversité / protection / relation plante insecte / pollinisateur

Zusammenfassung – Ökologische Aspekte des Schutzes von Bienen: Populationen, Arten, Artgemeinschaften. Die meisten der bereits ausgestorbenen oder vom Aussterben bedrohten Arten sind Insekten. Nichtsdestotrotz ist der Schutz von Insekten bisher weitgehend vernachlässigt worden. Die Befürchtungen jedoch, dass Pflanzen und ihre

Bestäuber Rückgänge verzeichnen und dementsprechend Ökosystemfunktionen negativ beeinflussen können, hat letztendlich die lokalen und globalen Bedrohungen der Bienendiversität ins Schlaglicht gerückt. Anzeichen für den Rückgang von Bienen häufen sich sowohl in taxonomischer als auch in geographischer Hinsicht. Wir geben hier eine Übersicht über die Rolle ökologischer Faktoren im Bienenschutz, wobei wir besonders die Frage der Arten, Populationen und Artgemeinschaften beleuchten.

Erfolgreicher Artenschutz erfordert zunächst ein grundlegendes Verständnis von zwischenartlichen Wechselwirkungen und von autökologischen Merkmalen (Abb. 1 und Tab. I). Das Aussterben von Bienenarten ist in vielen Fällen nicht dokumentiert und demzufolge sind vergleichende Analysen wichtig, um autökologische Faktoren erkennen zu können, die mit der Anfälligkeit zum Artenrückgang verknüpft sein können. Bienenpopulationen und Bienengemeinschaften zeichnen sich durch erhebliche raumzeitliche Schwankungen hinsichtlich ihrer Häufigkeit und Zusammensetzung aus, so dass die Variabilität dieser ökologischen Daten dazu führen kann, dass lange Beobachtungszeiträume notwendig sind, um faktische Rückgänge sichtbar machen zu können. Im Idealfall würde die Bestimmung kritischer Werte der Populationsgrößen und des Populationswachstums experimentelle Ansätze erfordern. In der Praxis werden aufgrund der logistischen Anforderungen, dem Problem fehlender Wiederholungen und den räumlichen Grössenordnungen jedoch meist Modellansätze bevorzugt, um Populationsrückgänge und Antworten auf regelnde Massnahmen sichtbar zu machen. Wir diskutieren hier die Erfassung von drei Schlüsselparametern für die Abschätzung von Populationsgrößen und Wachstumsraten: Ausbreitungsrate, Paarungssystem, sowie Prädatoren, Parasiten und Pathogene. Die Antwort von Einzeltieren, Populationen und Artgemeinschaften von Bienen auf anthropogen bedingte Umweltveränderungen ist primär bedingt durch die räumliche und zeitliche Verteilung von floralen sowie Nist- und Überwinterungsressourcen, die jeweils in Beziehung stehen zum Sammelverhalten und der Ausbreitungsfähigkeit der Bienen. Obwohl die primären Faktoren, die die Verteilung dieser Ressourcen bestimmen, bekannt sind, nämlich Habitatverlust, bzw. Fragmentierung, ergeben empirische Daten bezüglich der Antwort der Bienengemeinschaften auf diese Faktoren kein einheitliches Bild (Tab. II). Netzwerktheoretische Ansätze in Untersuchungen zur Architektur von Pflanzen/Bestäuber Netzwerken lassen jetzt Fortschritte erkennen und haben unsere Fähigkeit verbessert, Interaktionen zwischen Arten auf der Ebene von Gemeinschaften definieren und vorhersehen zu können. Mit Blick auf die globalen Umweltveränderungen wird die akkurate Abschätzung der Zahl, Stärke, Symmetrie und Variabilität dieser Interaktionen und ihr Einfluss auf die Toleranz

von Bienengemeinschaften gegen das Aussterben zunehmend an Bedeutung gewinnen. Da gegenwärtige Artenschutzmassnahmen im wesentlichen den Schutz von einzelnen Arten oder von Habitaten im Blick haben, werden ökologische Daten entscheidend sein für die Integration dieser beiden Managementstrategien auf einer breiteren, landschaftsorientierten Ebene von dynamischen und untereinander verbundenen Habitaten, die dann dazu beitragen können, dass Bienenschutz im Kontext globaler Umweltveränderungen möglich wird.

Artenschutz / Biodiversität / Population / Artgemeinschaft / Pflanzen-Bestäuber

REFERENCES

- Aizen M.A., Feinsinger P. (1994) Habitat Fragmentation, Native Insect Pollinators, and Feral Honey-Bees in Argentine Chaco Serrano, *Ecol. Appl.* 4, 378–392.
- Alcock J. (1997) Competition from large males and the alternative mating tactics of small males of Dawson's burrowing bee (*Amegilla dawsoni*) (Apidae, Apinae, Anthophorini), *J. Insect Behav.* 10, 99–113.
- Ashworth L., Aguilar R., Galetto L., Aizen M.A. (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J. Ecol.* 92, 717–719.
- Askew R.R. (1971) *Parasitic Insects*, Heinemann Educational Books, London, UK.
- Banaszak J. (1995) *Changes in Fauna of Wild Bees in Europe*, Pedagogical University, Bydgoszcz, Poland.
- Bascompte J., Jordano P. (2007) Plant-animal mutualistic networks: The architecture of biodiversity, *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593.
- Becker P., Moure J.S., Peralta F.J.A. (1991) More about euglossine bees in Amazonian forest fragments, *Biotropica* 23, 586–591.
- Biesmeijer J.C., Roberts S.P., Reemer M., Ohlemueller R., Edwards M., Peeters T., Schaffers A., Potts S.G., Kleukers R., Thomas C.D., Settele J., Kunin W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands, *Science* 313, 351–354.
- Blanchetot A. (1992) DNA fingerprinting analysis in the solitary bee *Megachile rotundata* – variability and nest mate genetic-relationships, *Genome* 35, 681–688.
- Bogusch P., Kratochvil L., Straka J. (2006) Generalist cuckoo bees (Hymenoptera: Apoidea: *Sphecodes*)

- are species-specialist at the individual level, *Behav. Ecol. Sociobiol.* 60, 422–429.
- Boomsma J.J., Schmid-Hempel P., Hughes W.O.H. (2005) Life histories and parasite pressure across the major groups of social insects, in: Fellowes M.D.E., Holloway G.J., Rolff J. (Eds.), *Insect Evolutionary Ecology*, CABI Publishing, London, pp. 139–176.
- Brady S.G., Sipes S., Pearson A., Danforth B.N. (2006) Recent and simultaneous origins of eusociality in halictid bees, *Proc. R. Soc. B Biol. Sci.* 273, 1643–1649.
- Brosi B.J., Daily G.C., Shih T.M., Oviedo F., Durán G. (2008) The effects of forest fragmentation on bee communities in tropical countryside, *J. Appl. Ecol.* 45, 773–783.
- Brussard P.F. (1991) The role of ecology in biological conservation, *Ecol. Appl.* 1, 6–12.
- Buchmann S.L., Nabhan G.P. (1996) *The Forgotten Pollinators*, Island Press, Washington, DC.
- Byrne A., Fitzpatrick Ú. (2009) Bee conservation policy at the global, regional and national levels, *Apidologie* 40, 194–210.
- Cane J.H. (1991) Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth, and climate, *J. Kans. Entomol. Soc.* 64, 406–413.
- Cane J.H. (2001) Habitat fragmentation and native bees: a premature verdict? *Conserv. Ecol.* 5.
- Cane J.H., Tepedino V.J. (2001) Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences, *Conserv. Ecol.* 5, <http://www.consecol.org/vol5/iss1/art1/> (accessed on 16 February 2009).
- Cane J.H., Sipes S. (2006) Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty, in: Waser N.M., Ollerton J. (Eds.), *Plant-pollinator interactions from specialization to generalization*, University of Chicago Press, Chicago, pp. 99–122.
- Cane J.H., Minckley R.L., Kervin L.J., Roulston T.H., Williams N.M. (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation, *Ecol. Appl.* 16, 632–644.
- Chacoff N.A., Aizen M.A. (2006) Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest, *J. Appl. Ecol.* 43, 18–27.
- Chapman R.E., Bourke A.F.G. (2001) The influence of sociality on the conservation biology of social insects, *Ecol. Lett.* 4, 650–662.
- Cornell H.V., Hawkins B.A. (2003) Herbivore responses to plant secondary compound: a test of phytochemical coevolution theory, *Am. Nat.* 161, 507–522.
- Cox-Foster D.L., Conlan S., Holmes E.C., Palacios G., Evans J.D., Moran N.A., Quan P.L., Briese T., Hornig M., Geiser D.M., Martinson V., van Engelsdorp D., Kalkstein A.L., Drysdale A., Hui J., Zhai J.H., Cui L.W., Hutchison S.K., Simons J.F., Egholm M., Pettis J.S., Lipkin W.I. (2007) A metagenomic survey of microbes in honey bee colony collapse disorder, *Science* 318, 283–287.
- Cresswell J.E., Osborne J.L., Goulson D. (2000) An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees, *Ecol. Entomol.* 25, 249–255.
- Crozier R.H., Pamilo P. (1996) *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection* Oxford University Press, New York.
- Danforth B.N. (1999) Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*, *Proc. R. Soc. B* 266, 1985–1994.
- Danforth B.N. (2002) Evolution of sociality in a primitively eusocial lineage of bees, *Proc. Natl Acad. Sci. USA* 99, 286–290.
- Danforth B.N., Ballard S., Ji L.J. (2003) Gene flow and population structure in an oligolectic desert bee, *Macrotera (Macroteropsis) portalis* (Hymenoptera: Andrenidae), *J. Kans. Entomol. Soc.* 76, 221–235.
- Defra (2005) *Environmental Stewardship*. Defra, London, UK, [online] www.defra.gov.uk/erdp/schemes/es/default.htm (accessed 16 February 2009).
- DeFries R.S., Foley J.A., Asner G.P. (2004) Land-use choices: balancing human needs and ecosystem function, *Frontiers Ecol. Environ.* 2, 249–257.
- Diaz S. et al. (2005) Biodiversity regulation of ecosystem services, in: Hassan R., Scholes R., Ash N. (Eds.), *Ecosystems and Human Well-Being: Current State and Trends*, Vol. 1, Island Press, Washington, DC, pp. 297–329.
- Dick C.W., Roubik D.W., Gruber K.F., Birmingham E. (2004) Long-distance gene flow and cross-Andean dispersal of lowland rainforest bees (Apidae: Euglossini) revealed by comparative mitochondrial DNA phylogeography, *Mol. Ecol.* 13, 3775–3785.
- Donaldson J., Nanni I., Zachariades C., Kemper J., Thompson J.D. (2002) Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa, *Conserv. Biol.* 16, 1267–1276.
- Dormann C.F., Schweiger O., Arens P., Augenstein I., Aviron S., Bailey D., Baudry J., Billeter R., Bugter R., Bukáček R., Burel F., Cerny M., De Cock R., De Blust G., DeFilippi R., Diekötter T., Dirksen J., Durka W., Edwards P.J., Frenzel M., Hamersky R., Hendrikx F., Herzog F., Klotz S., Koolstra B., Lausch A., Le Coeur D.,

- Liira J., Maelfait J.P., Opdam P., Roubalova M., Schermann-Legionnet A., Schermann N., Schmidt T., Smulders M.J.M., Speelmans M., Simova P., Verboom J., van Wingerden W., Zobel M. (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity, *Ecol. Lett.* 11, 234–244.
- Dukas R. (2005) Bumble bee predators reduce pollinator density and plant fitness, *Ecology* 86, 1401–1406.
- Durrer S., Schmid-Hempel P. (1995) Parasites and the regional distribution of bumblebee species, *Ecography* 18, 114–122.
- Eickwort G.C., Eickwort J.M., Gordon J., Eickwort M.A. (1996) Solitary behavior in a high altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae), *Behav. Ecol. Sociobiol.* 38, 227–233.
- Eickwort G.C., Ginsberg H.S. (1980) Foraging and mating-behavior in Apoidea, *Annu. Rev. Entomol.* 25, 421–446.
- Eltz T. (2004) Spatio-temporal variation of apine bee attraction to honeybaits in Bornean forests, *J. Trop. Ecol.* 20, 317–324.
- Eltz T., Bruhl C.A., van der Kaars S., Linsenmair K.E. (2002) Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia, *Oecologia* 131, 27–34.
- Eviner V.T., Likens G.E. (2008) The effects of pathogens on terrestrial ecosystem function, in: Ostfeld R., Keesing F., Eviner V.T. (Eds.), *Infectious Disease Ecology: The Effects of Ecosystems on Disease and of Disease on Ecosystems*, Princeton University Press, pp. 260–283.
- Falk S. (1991) A review of scarce and threatened bees, wasp and ants of Great Britain. Research and Survey in Nature Conservation No. 35, Nature Conservancy Council, UK.
- FAO (2008) Rapid Assessment of Pollinators' Status [online] <http://www.cbd.int/doc/case-studies/agr/cs-agr-fao.pdf> (accessed 16 February 2008).
- Fenster C.B., Armbruster W.S., Wilson P., Dudash M.R., Thomson J.D. (2004) Pollination syndromes and floral specialization, *Annu. Rev. Ecol. Evol. Syst.* 35, 375–403.
- Firbank L.G., Heard M.S., Woiwod I.P., Hawes C., Haughton A.J., Champion G.T., Scott R.J., Hill M.O., Dewar A.M., Squire G.R., May M.J., Brooks D.R., Bohan D.A., Daniels R.E., Osborne J.L., Roy D.B., Black H.I.J., Rothery P., Perry J.N. (2003) An introduction to the Farm-Scale Evaluations of genetically modified herbicide-tolerant crops, *J. Appl. Ecol.* 40, 2–16.
- Fisher D.O., Owens I.P.F. (2004) The comparative method in conservation biology, *Trends Ecol. Evol.* 19, 391–398.
- Fitzpatrick Ú., Murray T.E., Paxton R.J., Brown M.J.F. (2007) Building on IUCN regional red lists to produce lists of species of conservation priority: a model with Irish bees, *Conserv. Biol.* 5, 1324–1332.
- Fortuna M.A., Bascompte J. (2006) Habitat loss and the structure of plant-animal mutualistic networks, *Ecol. Lett.* 9, 278–283.
- Forup M.L., Henson K.S.E., Craze P.G., Memmott J. (2008) The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands, *J. Appl. Ecol.* 45, 742–752.
- Frankham R., Ballou J.D., Briscoe D.A. (2002) *Introduction to Conservation Genetics*, Cambridge University Press.
- Franzén M., Larsson M., Nilsson S.G. (2009) Small local population sizes and high habitat patch fidelity in a specialised solitary bee, *J. Insect Conserv.* 13, 89–95.
- Frommer U. (2008) Grundlagen der Ausbreitung und aktuellen nördlichen Verbreitung der Efeu-Seidenbiene *Colletes hederæ* Schmidt & Westrich, 1993 in Deutschland (Hymenoptera: Apidae), *Mitt. Int. Entomol. Ver.* 33, 59–74.
- Frommer U., Flügel H.-J. (2005) Zur Ausbreitung der Furchenbiene *Halictus scabiosæ* (Rossi, 1790) in Mitteleuropa unter besonderer Berücksichtigung der Situation in Hessen, *Mitt. Int. Entomol. Ver.* 30, 51–79.
- Gathmann A., Tschamtké T. (2002) Foraging ranges of solitary bees, *J. Anim. Ecol.* 71, 757–764.
- Gegear R.J., Otterstatter M.C., Thomson J.D. (2006) Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information, *Proc. R. Soc. Lond. B Biol. Sci.* 273, 1073–1078.
- Ghazoul J. (2005) Buzziness as usual? Questioning the global pollination crisis, *Trends Ecol. Evol.* 20, 367–373.
- Gilbert F., Gonzales A., Evans-Freke I. (1998) Corridors maintain species richness in the fragmented landscapes of a microecosystem, *Proc. R. Soc. Lond. B Biol. Sci.* 265, 577–582.
- Goulson D. (2003) *Bumblebees: their behaviour and ecology*, Oxford University Press, Oxford.
- Greenleaf S.S., Kremen C. (2006) Wild bees enhance honey bees' pollination of hybrid sunflower, *Proc. Natl Acad. Sci. USA* 103, 13890–13895.
- Greenleaf S.S., Williams N.M., Winfree R., Kremen C. (2007) Bee foraging ranges and their relationship to body size, *Oecologia* 153, 589–596.
- Haeseler V. (1973) Zur Kenntnis der Aculeaten- und Chrysididenfauna Schleswig-Holsteins und angrenzender Gebiete (Hymenoptera) 2. Beitrag, *Schr. Naturwiss. Ver. Schleswig-Holst.* 43, 51–60.

- Haeseler V. (1974) Aculeate Hymenopteren über Nord- und Ostsee nach Untersuchungen auf Feuerschiffen, *Entomol. Scand.* 5, 123–136.
- Haeseler V. (1976) Zur Aculeatenfauna der Nordfriesischen Insel Amrum (Hymenoptera), *Schr. Naturwiss. Vereins Schleswig-Holstein* 46, 59–78.
- Haeseler V. (1978) Zur Fauna der aculeaten Hymenopteren der Nordseeinsel Mellum. Ein Beitrag zur Besiedlung küstennaher Inseln, *Zool. Jb. Syst.* 105, 368–385.
- Hanski I. (1998) Metapopulation dynamics, *Nature* 396, 41–49.
- Hanski I., Pöyry J. (2006) Insect populations in fragmented habitats, in: Stewart A.J.A., New T.R., Lewis O.T. (Eds.), *Insect Conservation Biology*, R. Entomol. Soc. Int. Symp. on Insect Conservation Biology, University of Sussex, 12–14 September, 2005, CAB International, Wallingford, UK.
- Hedrick P.W., Parker J.D. (1997) Evolutionary genetics and genetic variation of haplodiploids and x-linked genes, *Annu. Rev. Ecol. Syst.* 28, 55–83.
- Hendrickx F., Maelfait J.P., van Wingerden W., Schweiger O., Speelman W., Aviron S., Augenstein I., Billeter R., Bailey D., Bukacek R., Burel F., Diekötter T., Dirksen J., Herzog F., Liira J., Roubalova M., Vandomme V., Bugter R. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural diversity, *J. Appl. Ecol.* 44, 340–351.
- Holzschuh A., Steffan-Dewenter I., Kleijn D., Tschamntke T. (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context, *J. Appl. Ecol.* 44, 41–49.
- Johansen C.A. (1977) Pesticides and pollinators, *Annu. Rev. Entomol.* 22, 177–192.
- Kathirithamby J. (1989) Review of the order Strepsiptera, *Syst. Entomol.* 14, 41–92.
- Kearns C.A., Inouye D.W., Waser N.M. (1998) Endangered mutualisms: the conservation of plant-pollinator interactions, *Annu. Rev. Ecol. Syst.* 29, 83–112.
- Kevan P.G. (1975) Forest application of the insecticide fenitrothion and its effect on wild bee pollinators (Hymenoptera: Apoidea) of lowbush blueberries (*Vaccinium* spp.) in: Southern New Brunswick, Canada, *Biol. Conserv.* 7, 301–309.
- Kim K.C., Byrne L. (2006) Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science, *Ecol. Res.* 21, 794–810.
- Kleijn D., Raemakers I. (2008) A retrospective analysis of pollen host plant use by stable and declining bumble bee species, *Ecology* 89, 1811–1823.
- Klein A.M., Steffan-Dewenter I., Buchori D., Tschamntke T. (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps, *Conserv. Biol.* 16, 1003–1014.
- Klein A.-M., Steffan-Dewenter I., Tschamntke T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees, *Proc. R. Soc. Lond. B Biol. Sci.* 270, 955–961.
- Knerer G. (1992) The biology and social behaviour of *Evylaeus malachurus* (K.) (Hymenoptera: Halictidae) in different climatic regions of Europe, *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere* 119, 261–290.
- Knight T.M., Chase J.M., Hillebrand H., Holt R.D. (2006) Predation on mutualists can reduce the strength of trophic cascades, *Ecol. Lett.* 9, 1173–1178.
- Koeniger G. (1991) Differences in filling of the spermatheca after natural and artificial insemination of the queen honeybee, *Apidologie* 22, 439–441.
- Koh L.P., Dunn R.R., Sodhi N.S., Colwell R.K., Proctor H.C., Smith V.C. (2004) Species coextinctions and the biodiversity crisis, *Science* 305, 1632–1634.
- Kosior A., Celary W., Olejniczak P., Fijał J., Król W., Solarz W., Plonka P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe, *Oryx* 41, 79–88.
- Kotiaho J.S., Kaitala V., Komonen A., Päivinen J. (2005) Predicting the risk of extinction from shared ecological characteristics, *Proc. Natl Acad. Sci. USA* 102, 1963–1967.
- Kratochwil A., Klatt M. (1989) Apoide Hymenopteren an Ruderalstellen der Stadt Freiburg i. Br. (BRD) – submediterrane Faunenelemente an Standorten kleinräumig hoher Persistenz, *Zool. Jahrb. Syst.* 116, 379–389.
- Kremen C., Ricketts T. (2000) Global perspectives on pollination disruptions, *Conserv. Biol.* 14, 1226–1228.
- Kremen C., Williams N.M., Thorp R.W. (2002) Crop pollination from native bees at risk from agricultural intensity, *Proc. Natl Acad. Sci. USA* 99, 16812–16816.
- Kremen C., Williams N.M., Bugg R.L., Fay J.P., Thorp R.W. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California, *Ecol. Lett.* 7, 1109–1119.
- Kremen C., Williams N.M., Aizen M.A., Gemmill-Herren B., LeBuhn G., Minckley R.L., Packer L., Potts S.G., Roulston T., Steffan-Dewenter I., Vásquez D.P., Winfree R., Adams L., Crone E.E., Greenleaf S.S., Keitt T.H., Klein A.-M., Regetz J., Ricketts T.H. (2007) Pollination and other ecosystem services provided by mobile organisms: a

- conceptual framework for the effects of land-use change, *Ecol. Lett.* 10, 299–314.
- Kuhlmann M. (2000) Die Struktur von Stechimmenzönosen (Hymenoptera Aculeata) ausgewählter Kalkmagerrasen des Diemeltales unter besonderer Berücksichtigung der Nutzungsgeschichte und des Requisitenangebotes, *Abh. Westf. Mus. Naturkd.* 62, 3–102.
- Kuhlmann M., Else G.R., Dawson A., Quicke D.L.J. (2007) Molecular, biogeographical and phonological evidence for the existence of three western European sibling species in the *Colletes succinctus* group (Hymenoptera: Apidae), *Org. Divers. Evol.* 7, 155–165.
- Lande R., Engen S., Saether B.-E. (2003) Stochastic population dynamics in ecology and conservation, Oxford University Press, USA.
- Larsen T.H., Williams N., Kremen C. (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning, *Ecol. Lett.* 8, 538–547.
- Lewis O.T. (2006) Climate change, species-area curves and the extinction crises, *Phil. Trans. R. Soc. B* 361, 163–171.
- Linsley E.G. (1958) The ecology of solitary bees, *Hilgardia* 27, 543–599.
- Mayer C., Kuhlmann M. (2004) Synchrony of pollinators and plants in the winter rainfall area of South Africa – observations from a drought year, *Trans. R. Soc. S. Afr.* 59, 55–57.
- Meek B., Loxton D., Sparks T., Pywell R., Pickett H., Nowakowski M. (2002) The effect of arable field margin composition on invertebrate biodiversity, *Biol. Conserv.* 106, 259–271.
- Memmott J., Waser N.M. (2002) Integration of alien plants into a native flower-pollinator visitation web, *Proc. R. Soc. Lond. B Biol. Sci.* 269, 2395–2399.
- Memmott J., Waser N.M., Price M.V. (2004) Tolerance of pollination networks to species extinctions, *Proc. R. Soc. Lond. B Biol. Sci.* 271, 2605–2611.
- Memmott J., Craze P.G., Waser N.M., Price M.V. (2007) Global warming and the disruption of plant-pollinator interactions, *Ecol. Lett.* 10, 710–717.
- Michener C.D. (1974) The social behavior of the bees, Harvard University Press.
- Michener C.D. (2007) The bees of the world, 2nd ed., Johns Hopkins Press, Baltimore.
- Minckley R.L., Cane J.H., Kervin L. (2000) Origins and ecological consequences of pollen specialization among desert bees, *Proc. R. Soc. Lond. B Biol. Sci.* 267, 265–271.
- Minckley R.L., Weislo W.T., Yanega D., Buchmann S.L. (1994) Behavior and Phenology of a Specialist Bee (*Dieunomia*) and Sunflower (*Helianthus*) Pollen Availability, *Ecology* 75, 1406–1419.
- Moldenke A.R. (1979) Host-plant coevolution and the diversity of bees in relation to the flora of North America, *Phytologia* 43, 357–419.
- Morandin L.A., Winston M.L. (2005) Wild bee abundance and seed production in conventional, organic, and genetically modified canola, *Ecol. Appl.* 15, 871–881.
- Moretti M., de bello F., Roberts S.P.M., Potts S.G. (2009) Taxonomical versus functional responses of bee communities to fire in two contrasting climatic regions, *J. Anim. Ecol.* 78, 98–108.
- Moritz R.F.A., Kraus F.B., Kryger P., Crewe R.M. (2007) The size of wild honeybee populations (*Apis mellifera*) and its implications for the conservation of honeybees, *J. Insect Conserv.* 11, 391–397.
- Müller A. (1996) Host-plant specialization in western palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae), *Ecol. Monogr.* 66, 235–257.
- Müller A., Kuhlmann M. (2008) Pollen hosts of western palaeartic bees of the genus *Colletes* (Hymenoptera: Colletidae) – the Asteraceae paradox, *Biol. J. Linn. Soc.* 95, 719–733.
- Müller A., Diener S., Schnyder S., Stutz K., Sedivy C., Dorn S. (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships, *Biol. Conserv.* 130, 604–615.
- National Research Council of the National Academies (2006) Status of Pollinators in North America. National Academy Press, Washington, DC.
- Norris K. (2004) Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm, *J. Appl. Ecol.* 41, 413–426.
- O’Grady J.J., Reed D.H., Brook B.W., Frankham R. (2004) What are the best correlates of predicted extinction risk? *Biol. Conserv.* 118, 513–520.
- O’Toole C., Raw A. (1991) Bees of the World, Sterling Publishing, New York.
- Okuyama T., Holland J.N. (2008) Network structural properties mediate the stability of mutualistic communities, *Ecol. Lett.* 11, 208–216.
- Oldroyd B.P., Nanork P. (2009) Conservation of Asian honeybees, *Apidologie*, 40, 296–312.
- Packer L., Owen R. (2001) Population genetic aspects of pollinator decline, *Conserv. Ecol.* 5.
- Packer L., Zayed A., Grixti J.C., Ruz L., Owen R.E., Vivallo F., Toro H. (2005) Conservation genetics of potentially endangered mutualisms: reduced

- levels of genetic variation in specialist versus generalist bees, *Conserv. Biol.* 19, 195–202.
- Pamilo P., Crozier R.H. (1997) Population biology of social insect conservation, *Mem. Mus. Victoria* 56, 411–419.
- Pamilo P., Gertsch P., Thorén P., Seppä P. (1997) Molecular population genetics of social insects, *Annu. Rev. Ecol. Syst.* 28, 1–25.
- Paxton R.J. (2005) Male mating behaviour and mating systems of bees: an overview, *Apidologie* 36, 145–156.
- Paxton R.J., Fries I., Pieniazek N.J., Tengö J. (1997) High incidence of infection of an undescribed microsporidium (Microspora) in the communal bee *Andrena scotica* (Hymenoptera, Andrenidae), *Apidologie* 28, 129–141.
- Paxton R.J., Giovanetti M., Andrietti F., Scamoni E., Scanni B. (1999) Mating in a communal bee *Andrena agillissima* (Hymenoptera: Andrenidae), *Ecol. Ethol. Evol.* 11, 371–382.
- Paxton R.J., Thorén P.A., Estoup A., Tengo J. (2001) Queen-worker conflict over male production and the sex ratio in a facultatively polyandrous bumblebee, *Bombus hypnorum*: the consequences of nest usurpation, *Mol. Ecol.* 10, 2489–2498.
- Paxton R.J., Ayasse M., Field J., Soro A. (2002) Complex sociogenetic organization and reproductive skew in a primitively eusocial sweat bee, *Lasioglossum malachurum*, as revealed by microsatellites, *Mol. Ecol.* 11, 2405–2416.
- Pekkarinen A. (1997) Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea), *Entomol. Fenn.* 8, 205–214.
- Petanidou T., Ellis W.N., Ellisadam A.C. (1995) Ecogeographical patterns in the incidence of brood parasitism in bees, *Biol. J. Linn. Soc.* 55, 261–272.
- Petanidou T., Kallimanis A.S., Tzanopoulos J., Sgardelis S.P., Pantis J.D. (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization, *Ecol. Lett.* 11, 564–575.
- Peters G. (1972) Ursachen für den Rückgang der seltenen heimischen Hummelarten (Hym., *Bombus* et *Psithyrus*), *Entomol. Ber.* 1972, 85–90.
- Peters J.M., Queller D.C., Imperatriz-Fonseca V.L., Roubik D.W., Strassmann J.E. (1999) Mate number, kin selection and social conflicts in stingless bees and honeybees, *Proc. R. Soc. Lond. B Biol. Sci.* 266, 379–384.
- Pimm S.L., Ayres M., Balmford A., Branch G., Brandon K., Brooks T., Bustamante R., Costanza R., Cowling R., Curran L.M., Dobson A., Farber S., da Fonseca G.A., Gascon C., Kitching R., McNeely J., Lovejoy T., Mittermeier R.A., Myers N., Patz J.A., Raffle B., Rapport D., Raven P., Roberts C., Rodriguez J.P., Rylands A.B., Tucker C., Safina C., Samper C., Stiassny M.L., Supriatna J., Wall D.H., Wilcove D. (2001) Can we defy nature's end? *Science* 293, 2207–2208.
- Pohl H., Beutel R.G. (2008) The evolution of Strepsiptera (Hexapoda), *Zoology* 111, 318–338.
- Potts S.G., Willmer P.G. (1997) Abiotic and biotic factors influencing nest-site selection in *Halictus rubicundus*, a ground nesting halictine bee, *Ecol. Entomol.* 22, 319–328.
- Potts S.G., Vulliamy B., Dafni A., Ne'eman G., Willmer P. (2003) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84, 2628–2642.
- Potts S.G., Vulliamy B., Roberts S., O'Toole C., Dafni A., Ne'eman G., Willmer P. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape, *Ecol. Entomol.* 30, 78–85.
- Potts S.G., Petanidou T., Roberts S., O'Toole C., Hulbert A., Willmer P. (2006) Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape, *Biol. Conserv.* 129, 519–529.
- Potts S.G., Woodcock B.A., Roberts S.P.M., Tscheulin T., Ramsay A.J., Pilgrim E., Brown V.K., Tallowin J.R. (2009) Enhancing pollinator biodiversity in intensive grasslands, *J. Appl. Ecol.*, DOI 10.1111/j.1365-2664.2009.01609.x.
- Powell J.A., Mackie R.A. (1966) Biological relationships of moth and *Yucca whipplei* (Lepidoptera: Gelechiidae, Blastobasidae, Prodoxidae), *Univ. Calif. Publ. Entomol.* 42, 1–59.
- Powell A.H., Powell G.V.N. (1980) Population dynamics of male euglossine bees in Amazonian forest fragments, *Biotropica* 19, 176–179.
- Praz C.J., Müller A., Dorn S. (2008) Specialized bees fail to develop on no-host pollen: do plants chemically protect their pollen? *Ecology* 89, 795–804.
- Price P.W., Westoby M., Rice B., Atsatt P.R., Fritz R.S., Thompson J.N., Mobley K. (1986) Parasite Mediation in Ecological Interactions, *Annu. Rev. Ecol. Syst.* 17, 487–505.
- Price P.W., Westoby M., Rice B. (1988) Parasite-Mediated Competition – Some Predictions and Tests, *Am. Nat.* 131, 544–555.
- Rasmont P. (1988) Monographie écologique et zoogéographique des bourdons de Belgique et de Belgique (Hymenoptera, Apidae, Bombinae), PhD thesis, Faculté des Sciences Agronomique de l'État, Gembloux, Belgium.
- Rasmont P., Pauly A., Terzo M., Patiny S., Michez D., Iserbyt S., Barbier Y., Haubruge E. (2005) The

- survey of wild bees (Hymenoptera, Apoidea) in Belgium and France, FAO report [online] <http://www.fao.org/ag/AGP/AGPS/C-CAB/Castudies/pdf/1-010.pdf> (accessed on 9 February 2009).
- Ricketts T. (2004) Do tropical forest fragments enhance pollinator activity in nearby coffee crops, *Conserv. Biol.* 18, 1–10.
- Robertson C. (1925) Heterotropic bees, *Ecology* 6, 412–436.
- Roubik D.W. (1989) *Ecology and natural history of tropical bees*, Cambridge University Press, Cambridge.
- Roubik D.W. (2001) Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology* 5, <http://www.consecol.org/vol5/iss1/art2/> (accessed on 16 February 2009).
- Sakagami S.F., Munakata M. (1972) Distribution and bionomics of a transpalearctic eusocial halictine bee, *Lasioglossum (Evylaeus) calceatum*, in northern Japan, with reference to its solitary life at high latitude, *J. Fac. Sci. Hokkaido Univ. Ser VI Zool.* 18, 411–439.
- Samejima H., Marzuki M., Nagamitsu T., Nakasizuka T. (2004) The effects of human disturbance on a stingless bee community in a tropical rainforest, *Biol. Conserv.* 120, 577–587.
- Sammataro D., Gerson U., Needham G. (2000) Parasitic mites of honey bees: life history, implications and impact, *Annu. Rev. Entomol.* 45, 519–548.
- Schlüns H., Moritz R.F.A., Neumann P., Kryger P., Koeniger G. (2005) Multiple nuptial flights, sperm transfer and the evolution of extreme polyandry in honeybee queens, *Anim. Behav.* 70, 125–131.
- Schmid-Hempel P. (2001) On the evolutionary ecology of host-parasite interactions: addressing the question with regard to bumblebees and their parasites, *Naturwissenschaften* 88, 147–158.
- Schmid-Hempel R., Schmid-Hempel P. (2000) Female mating frequencies in *Bombus* spp. from Central Europe, *Insectes Soc.* 47, 36–41.
- Schmidt J.O., Thoenes S.C. (1992) Criteria for nest site selection in honey-bees (Hymenoptera: Apidae) – preference between pheromone attractants and cavity shapes, *Environ. Entomol.* 21, 1130–1133.
- Schoener T.W. (1979) Generality of the size-distance relation in models of optimal foraging, *Am. Nat.* 114, 902–914.
- Schtickzelle N., Baguette M. (2004) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS, *Oikos* 104, 277–290.
- Schultz C.B., Hammond P.C. (2003) Using population viability analysis to develop recovery criteria for endangered insects: case study of the Fender's Blue Butterfly, *Conserv. Biol.* 17, 1372–1385.
- Schweiger O., Maelfait J.P., Van Wingerden W., Hendrikx F., Billeter R., Speelmans M., Augenstein I., Aukema B., Aviron S., Bailey D., Bukacek R., Burel F., Diekötter T., Dirksen J., Frenzel M., Herzog F., Liira J., Roubalova M., Bugter R. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales, *J. Appl. Ecol.* 42, 1129–1139.
- Scott V.L. (1994) Phenology and trap selection of three species of *Hylaeus* (Hymenoptera, Colletidae) in upper Michigan, *Gt. Lakes Entomol.* 27, 39–47.
- Scott V.L., Kelley S.T., Strickler K. (2000) Reproductive biology of two *Coelioxys* cleptoparasites in relation to their Megachile hosts (Hymenoptera: Megachilidae), *Ann. Entomol. Soc. Am.* 93, 941–948.
- Simberloff D. (1988) The contribution of population and community biology to conservation science, *Annu. Rev. Ecol. Syst.* 19, 473–511.
- Simonthomas R.T., Simonthomas A.M.J. (1980) *Philanthus triangulum* and its recent eruption as a predator of honeybees in an Egyptian oasis, *Bee World* 61, 97–107.
- Singer M.S. (2008) Evolutionary ecology of polyphagy, in: Tilmon K.J. (Ed.), *Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects*, University of California Press, Berkeley, pp. 29–42.
- Smith A.R., Wcislo W.T., O'Donnell S. (2007) Survival and productivity benefits to social nesting in the sweat bee *Megalopta genalis* (Hymenoptera: Halictidae), *Behav. Ecol. Sociobiol.* 61, 1111–1120.
- Soucy S.L. (2002) Nesting biology and socially polymorphic behavior of the sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae), *Ann. Entomol. Soc. Am.* 95, 57.
- Staples D.F., Taper M.L., Shepard B.B. (2005) Risk-based viable population monitoring, *Conserv. Biol.* 19, 1908–1916.
- Steffan-Dewenter I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows, *Conserv. Biol.* 17, 1036–1044.
- Steffan-Dewenter I., Münzenberg U., Bürger C., Thies C., Tschardt T. (2002) Scale-dependent effects of landscape context on three pollinator guilds, *Ecology* 83, 1421–1432.
- Steffan-Dewenter I., Tschardt T. (1999) Effects of habitat isolation on pollinator communities and seed set, *Oecologia* 121, 432–440.

- Steffan-Dewenter I., Tscharntke T. (2001) Succession of bee communities on fallows, *Ecography* 24, 83–93.
- Steffan-Dewenter I., Tscharntke T. (2002) Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review, *Biol. Conserv.* 104, 275–284.
- Steffan-Dewenter I., Westphal C. (2008) The interplay of pollinator diversity, pollination services and landscape change, *J. Appl. Ecol.* 45, 737–741.
- Steffan-Dewenter I., Potts S.G., Packer L. (2005) Pollinator diversity and crop pollination services are at risk, *Trends Ecol. Evol.* 20, 651–652.
- Stork N.E., Lyal C.H.C. (1993) Extinction or Co-Extinction Rates, *Nature* 366, 307–307.
- Stout J.C., Morales C.L. (2009) Ecological impacts of invasive alien species on bees, *Apidologie* 40, 388–409.
- Strickler K. (1979) Specialization and foraging efficiency of solitary bees, *Ecology* 60, 998–1009.
- Tauber M.J., Tauber C.A., Nyrop J.P., Villani M.G. (1998) Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms, *Environ. Entomol.* 27, 523–530.
- Tewksbury J.J., Levey D.J., Haddad N.M., Sargent S., Orrock J.L., Weldon A., Danielson B.J., Brinkerhoff J., Damschen E.I., Townsend P. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes, *Proc. Natl Acad. Sci. USA* 99, 12923–12926.
- Thomas C.D., Cameron A., Green R.E., Bakkenes M., Beaumont L.J., Collingham Y.C., Erasmus B.F.N., de Siqueira M.F., Grainger A., Hannah L., Hughes L., Huntley B., van Jaarsveld A.S., Midgley G.F., Miles L., Ortega-Huerta M.A., Peterson A.T., Phillips O.L., Williams S.C. (2004) Extinction risk from climate change, *Nature* 427, 577–280.
- Thompson J.N. (2005) *The Geographic Mosaic of Coevolution*, University of Chicago Press, Chicago, Illinois.
- Tilman D., Reich P.B., Knops J., Wedin D., Mielke T. (2001) Diversity and productivity in a long-term grassland experiment, *Science* 294, 843–845.
- Tonhasca A., Blackmer J.L., Albuquerque G.S. (2002) Abundance and diversity of euglossine bees in the fragmented landscape of the Brazilian Atlantic forest, *Biotropica* 34, 416–422.
- Tscharntke T., Brandl R. (2004) Plant-insect interactions in fragmented landscapes, *Annu. Rev. Entomol.* 49, 405–430.
- Tscharntke T., Klein A.M., Kruess A., Steffan-Dewenter I., Thies C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management, *Ecol. Lett.* 8, 857–874.
- Tylianakis J.M., Klein A.-M., Tscharntke T. (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient, *Ecology* 86, 3296–3302.
- Tylianakis J.M., Didham R.K., Bascompte J., Wardle D.A. (2008) Global change and species interactions in terrestrial ecosystems, *Ecol. Lett.* 11, 1351–1363.
- Vandergast A.G., Gillespie R.G. (2004) Effects of natural forest fragmentation on a Hawaiian spider community, *Environ. Entomol.* 33, 1296–1305.
- Vulliamy B., Potts S.G., Willmer P.G. (2006) The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape, *Oikos* 114, 529–543.
- Wagner A.C.W. (1938) Die Stechimmen und Goldwespen des westlichen Norddeutschland, *Verh. Ver. Naturwiss. Heimatforsch. Hamburg* 26, 94–153.
- Wcislo W.T. (1987) The roles of seasonality host synchrony and behavior in the evolutions and distributions of nest parasites in Hymenoptera (Insecta). With special reference to bees (Apoidea), *Biol. Rev. (Camb.)* 63, 515–544.
- Wcislo W.T., Cane J.H. (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies, *Annu. Rev. Entomol.* 41, 257–286.
- Westbury D.B., Woodcock B.A., Harris S.J., Brown V.K., Potts S.G. (2008) The effect of seed mix and management on the abundance of desirable and pernicious unsown species in field margin communities, *Weed Sci.* 48, 113–123.
- Westphal C., Steffan-Dewenter I., Tscharntke T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale, *Ecol. Lett.* 6, 961–965.
- Westphal C., Steffan-Dewenter I., Tscharntke T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees, *J. Appl. Ecol.* 46, 187–193.
- Westrich P. (1989) *Die Wildbienen Baden-Württembergs*, Stuttgart, Ulmer.
- Westrich P. (1996) Habitat requirements of central European bees and the problems of partial habitats, in: Matheson A., Buchmann S.L., Westrich P., Williams, I.H. (Eds.), *The conservation of bees*, Academic Press, London, pp. 1–16.
- Williams I.H., Corbet S.A., Osborne J.L. (1991) Beekeeping, wild bees and pollination in the European Community, *Bee World* 72, 170–180.
- Williams N.M. (2003) Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae), *Oecologia* 134, 228–237.

- Williams N.M., Kremen C. (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape, *Ecol. Appl.* 17, 910–921.
- Williams N.M., Minckley R.L., Silveira F.A. (2001) Variation in native bee faunas and its implications for detecting community change, *Conserv. Ecol.* 5, <http://www.consecol.org/vol5/iss1/art7/> (accessed on 16 February 2009).
- Williams P.H. (1986) Bumble bees and their decline in Britain. Central Association of Beekeepers, UK.
- Williams P.H., Osborne J. (2009) Bumblebee vulnerability and conservation world-wide, *Apidologie*, 40, 367–387.
- Winfree R., Griswold T., Kremen C. (2007) Effect of human disturbance on bee communities in a forested ecosystem, *Conserv. Biol.* 21, 213–223.
- Winfree R., Williams N.M., Gaines H., Ascher J.S., Kremen C. (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA, *J. Appl. Ecol.* 45, 793–802.
- Wülker W. (1964) Parasite-induced changes of internal and external sex characters in insects, *Exp. Parasitol.* 15, 561–597.
- Zammit J., Hogendoorn K., Schwarz M.P. (2008) Strong constraints to independent nesting in a facultatively social bee: quantifying the effects of enemies-at-the-nest, *Insectes Soc.* 55, 74–78.
- Zayed A. (2009) Bee genetics and conservation, *Apidologie*, 40, 237–262.
- Zayed A., Packer L., Grixti J.C., Ruz L., Owen R.E., Toro H. (2005) Increased genetic differentiation in a specialist versus a generalist bee: implications for conservation, *Conserv. Genet.* 6, 1017–1026.