Native Pollinators in Anthropogenic Habitats

Rachael Winfree, Ignasi Bartomeus,
and Daniel P. Cariveau

Department of Entomology, Rutgers University, New Brunswick, NJ 08901;
email: rwinfree@rutgers.edu, ibart@rci.rutgers.edu, cariveau@rci.rutgers.edu

Annu. Rev. Ecol. Evol. Syst. 2011. 42:1–22

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-102710-145042

1543-592X/11/1201-0001$20.00

Keywords

bat, bee, bird, butterfly, disturbance, fly, land-use change, moth, pollination

Abstract

Animals pollinate 87% of the world's flowering plant species. Therefore, how pollinators respond to human-induced land-use change has important implications for plants and the species that depend on them. Here, we synthesize the published literature on how land-use change affects the main groups of pollinators: bees, butterflies, flies, birds, and bats. Responses to land-use change are predominantly negative but are highly variable within and across taxa. The directionality of pollinator response varies according to study design, with comparisons across gradients in surrounding landscape cover finding largely negative responses and comparisons across local land-use types finding largely positive responses. Furthermore, among the studies using landscape designs, most were performed in systems where land-use change is extreme, and such studies find stronger negative effects than those performed in more moderate systems. Across multiple taxa, dietary specialists show greater sensitivity to land use than do generalists. There is a need for studies of pollinator species composition and relative abundance, rather than simply species richness and aggregate abundance, to identify the species that are lost and gained with increasing land-use change.

1. INTRODUCTION

Land-use change: human modification of the terrestrial land surface, encompassing the loss and fragmentation of natural habitats

Ecosystem functions: ecological processes that naturally occur within ecosystems, for example, pollination, plant productivity, or nutrient cycling

Anthropogenic habitats: human-modified habitats

In an era of increasing anthropogenic land-use change, it is important to understand the impacts of such land use on species groups that provide critical ecosystem functions. Pollinators are one such group: Eighty-seven percent of the world's wild plants, or roughly 308,000 species, are pollinated by animals (Ollerton et al. 2011). Although many animal-pollinated plants can self-pollinate to some degree, thus lessening the extent of short-term reliance on pollinators, all rely on pollinators in the long term for genetic exchange among individuals. The interactions between plants and pollinators are increasingly situated within ecosystems dominated by human land use. As of 2000, 40% of Earth's ice-free land area is being directly used by humans, and an additional 37% is surrounded by human-modified areas (Ellis et al. 2010). Human land use is predicted to increase rapidly over the next few decades as the human population grows (Tilman et al. 2001). Therefore, how pollinators respond to land-use change has important implications for much of the world's flora.

Many scientists are concerned that pollinators are in decline globally (Potts et al. 2010). However, firm conclusions are hampered by a lack of long-term monitoring data that could reveal trends in pollinator populations over time. In the European Union (EU), where pollinator population status has been best evaluated, some but not all taxa are clearly declining. Across multiple EU countries, 37–65% of bee species are considered to be of conservation concern (Patiny et al. 2009), and in the United Kingdom (UK), 71% of butterfly species have declined to some extent over the past 20 years (Thomas et al. 2004). In North America, a recent National Research Council report concluded that there is evidence of decline for particular bumblebee, butterfly, bat, and hummingbird species, but that for most pollinator species "the paucity of long-term population data and the incomplete knowledge of even basic taxonomy and ecology make definitive assessment of status exceedingly difficult" (NRC 2007, p. 7). The lack of biological knowledge about many pollinator species contributes to their lack of formal protection. For example, only two species of bee are on the Red List of threatened species established by the International Union for Conservation of Nature (IUCN), although multiple species are known to be declining precipitously (Williams & Osborne 2009). Anthropogenic land use has been identified as a principal cause of decline for many threatened species, and it may be causal for pollinators as well (Pereira et al. 2010, Potts et al. 2010).

The objective of this review is to synthesize the published literature across pollinator taxa, geographic regions, types of anthropogenic habitats, and research designs to look for general patterns in pollinator response to land-use change. Given the crucial role that pollinators play in ecosystems, the literature on how they are affected by land-use change is surprisingly recent. As of 1993, there were only five published studies on pollinators and human-induced loss of natural habitats (Rathcke & Jules 1993), and in 1998 an influential review on plant-pollinator interactions concluded that "the response of insects to fragmentation is poorly understood" (Kearns et al. 1998, p. 89). Since that time, the literature has grown enormously. There have been recent reviews of pollinator conservation and restoration (Potts et al. 2010, Menz et al. 2011) and a synthetic analysis investigating how land use affects crop pollinators (Ricketts et al. 2008). Other reviews and meta-analyses have focused exclusively on one taxon, investigating responses to tropical deforestation in butterflies (Koh 2007), the role of resources and natural enemies in regulating bee populations (Roulston & Goodell 2011), bee conservation and restoration (Murray et al. 2009, Winfree 2010), or bee community responses to anthropogenic disturbances (Winfree et al. 2009) and the role of species traits in moderating bee responses to disturbance (Williams et al. 2010). The distinguishing feature of our review is that we synthesize the published literature on multiple pollinator taxa in terms of responses to land-use change. Our review of the published literature yielded 265 published

Table 1 Directionality of changes in pollinator outcomes with increasing human land use. Cells record counts for the directionality of changes in pollinator abundance and species richness with increasing human land use. All studies are listed in Supplemental Table 1. Responses were classed as negative or positive when $P \leq 0.10$. Nondirectional responses are included in the neutral category

Supplemental Material

	Directionality of pollinator response			
	Negative	Neutral	Positive	Negative:positive
Bees	81	94	27	3.0:1
Butterflies	88	88	47	1.9:1
Syrphid flies	18	14	14	1.3:1
Birds	24	20	30	0.8:1
Bats	9	12	20	0.5:1

studies, contributing a total of 674 measures of pollinator response to anthropogenic land use. Information on each of these studies is available in **Supplemental Table 1.** (Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**.) A summary table by pollinator taxon shows that pollinator response to land-use change is predominantly negative, but highly variable (**Table 1**). Our review focuses on possible reasons for this variability. We consider three broad classes of explanation:

1. Characteristics of land-use change, including the type and extent of change.
2. Characteristics of pollinators, including species traits.
3. Research methods and biases.

As pollinators are defined by their function and are taxonomically diverse, we begin with an introduction to the major groups of pollinators.

2. WHO ARE THE POLLINATORS?

There is at present no quantitative evaluation of the relative importance of the different pollinating taxa to pollinating the worlds' flora. However, most pollination ecologists would agree that bees (series Apiformes) are the predominant pollinators for most plants and ecosystems. Bees are often the most frequent visitors of flowers (Neff & Simpson 1993), which makes them likely the most important pollinators as well, insofar as visitation rate is a strong predictor of pollination (Vázquez et al. 2005). The predominance of bees as pollinators is attributable to the fact that all 20,000 species are obligate florivores and both larval and adult life stages feed on floral products. In contrast, in all other pollinator taxa, only a subset of species visit flowers, and florivory is confined to the adult stage (Michener 2007). Female bees of nonparasitic species spend much of their adult lives collecting pollen to provision their offspring and have specialized pollen-collecting structures and behaviors, in contrast to most other pollinator taxa. Bees are present in a wide variety of terrestrial habitats worldwide.

Flies (order Diptera) are the second most frequent visitors to flowers overall (Larson et al. 2001), and they often outnumber bees in lower-temperature situations such as high latitude areas (Elberling & Olesen 1999). Although flies are a diverse group of over 150,000 species, and species from over 70 families have been observed visiting flowers in North America alone (Larson et al. 2001), the frequent flower visitors are concentrated in only three families: Syrphidae (hoverflies or flower flies; herein syrphid flies), Bombyliidae (bee flies), and Tachinidae (tachinid flies). Of these three groups, the syrphid flies are likely the most important flower visitors (Larson et al. 2001). Syrphid flies are found in a variety of habitats throughout the world and are the main group that has been studied in the context of land-use change; thus, our review of flies focuses on the syrphid flies. In nearly all of the 6,000 syrphid fly species, adults consume nectar, and some species consume pollen.

Butterflies and moths (Lepidoptera) are a diverse group of 300,000 species of which only an estimated 14,500 are butterflies, with the remainder being moths. Many species are nectarivorous; but with a few exceptions, they do not consume pollen. Some species do not feed on flowers, but rather fruit sap or blood, or do not feed at all as adults (Scoble 1995). The nectarivorous and, therefore, pollinating taxa are concentrated in the moth families Sphingidae (hawk moths), Noctuidae (owlet moths), and Geometridae (geometer moths), and the butterfly families Hesperiidae (skippers) and Papilionoidea (common butterflies); thus, these families are the focus of this review. All of the nectarivorous families are represented worldwide but reach their maximum diversity in the tropics (Scoble 1995). Although comprehensive data on this point are lacking, it is thought that for most plant species, butterflies visit flowers less frequently than do bees and may also deposit less pollen per visit (e.g., Sahli & Conner 2007). However, some studies suggest that butterflies and moths carry pollen farther than other insects, and this long-distance pollen transfer could have important genetic consequences for plants (Herrera 1987).

Among the vertebrates, pollinators are primarily found in particular families of birds and bats. There are six main families of nectar-feeding birds (Fleming & Muchhala 2008). The most speciose group is the Trochilidae (Hummingbirds; 328 flower-visiting species), which are found only in North and South America. The Nectariniidae (sunbirds and flowerpeckers; 174 flower-visiting species), Psittacidae (lorikeets; 53 flower-visiting species), and Meliphagidae (honeyeaters; 176 flower-visiting species) are primarily tropical forest species and are found in Australia, Africa, and Asia (Fleming & Muchhala 2008). Although particular species in other families are known to visit flowers, the vast majority of species do not do so; we therefore focus our review on the families named above.

Two families of bats contain flower-visiting species: the leaf-nosed bats (Phyllostomidae; 38 flower-visiting species) and the fruit bats (Pteropidae; 15 flower-visiting species; Fleming & Muchhala 2008). The Phyllostomidae are found in North and South America, and most species occur in tropical forests. Flower-visiting Pteropidae occur in Asia and Australia, and there is one species in Africa. Flowers visited by bats are generally morphologically distinct and night-blooming, and are often not visited by taxa other than bats (Fleming et al. 2009). **Figure 1** shows representatives of the main pollinator taxa.

Occasional pollinators are found in other, widely divergent taxonomic groups. Beetles (order Coleoptera) in at least 17 families visit specialized beetle-pollinated plants from 34 different plant families, and species in another 4 beetle families are more generalist visitors (Bernhardt 2000). Similarly, wasps (order Hymenoptera), particularly in the families Vespidae, Scoliidae, and Pompilidae, are common flower visitors, and the Agaonidae have a highly specialized pollinating association with figs (Weiblen 2002). Ants (Hymenoptera, Formicidae) are known to visit at least 20 plant species (Rico-Gray & Oliveira 2006), and thrips (Thysanoptera) may be important for specific plant taxa (Mound 2005). Nonflying mammals such as marsupials, rodents, and primates visit at least 85 species of plants globally (Carthew & Goldingay 1997). We were unable to find any further quantitative information on the global importance of the above taxa as pollinators. Because studies reporting land-use change effects on these incidental taxa are scarce, we mention them only tangentially in this review. More studies documenting the contribution of these groups (e.g., generalist beetle visitors) and how they respond to land-use change are needed.

Even within the main pollinator taxa enumerated above, the number of studies reporting responses to land-use change varies widely across taxa. Bees and butterflies dominate the literature, whereas published studies of syrphids, birds, and bats are scarcer (**Table 1**). Hereafter, we

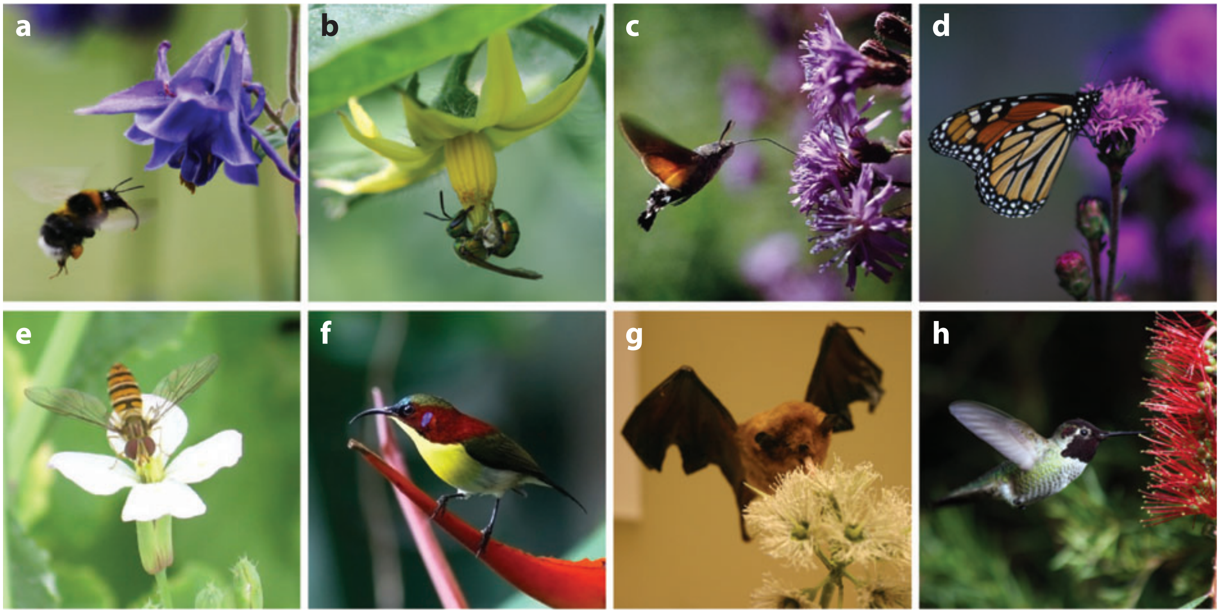

Figure 1

Examples of the primary pollinator taxa. (*a*) Bumblebee (*Bombus* sp.), (*b*) solitary bee in the tribe Augochlorini, (*c*) hawk moth (*Macroglossum stellatarum*, Sphingidae), (*d*) monarch butterfly (*Danaus plexippus*, Nymphalidae), (*e*) syrphid fly (Syrphidae), (*f*) sunbird (*Aethopyga bella*, Nectariniidae), (*g*) bat (*Glossophaga soricina*, Phyllostomidae), and (*h*) hummingbird (*Calypte anna*, Trochilidae). Photo credits: L. Mandle, I. Bartomeus, and the following Wikimedia Commons and NBII LIFE authors: Roo72, Mh-k, J.J. Mosesso, Llimchiu, R. Somma and Mbz l.

combine responses of pollinating birds and bats as there are relatively few studies of these groups, and they inhabit similar ecosystems (tropical forests) and exhibit similar responses to land-use change. Lastly, there is a geographic bias in the published literature, such that studies conducted in Europe or North America account for 52% of all recorded responses, whereas tropical countries account for 39%, and India, Russia, and China are particularly underrepresented as they collectively account for <1%. Consequently, our review of necessity reflects the information that is available.

3. POLLINATOR RESPONSE TO LAND-USE CHANGE: TERMINOLOGY AND METHODS

Our literature review was conducted using ISI Web of Science searches through December 2010. Our criteria for inclusion in our review were that a study (*a*) measured pollinator outcomes such as abundance, species richness, diversity, community composition, or genetic diversity as a function of treatments related to anthropogenic land use, (*b*) was replicated, and (*c*) reported statistical results or data. For studies of vertebrates and tropical butterflies, for which a species within a given taxonomic group can be either flower-visiting or not, we recorded results for the flower visitors alone whenever these were distinguished by the researchers. In some studies it was not possible to distinguish the flower visitors from other guilds, most notably in studies of tropical butterfly families that include both flower-visiting and fruit-feeding species. Given the paucity of published work on these groups, we included these studies so long as pollinating taxa were the predominant members of the studied group. We focus on native pollinators, thus excluding studies of domesticated pollinators such as the honey bee (*Apis mellifera*) and of invasive pollinator species, which may show idiosyncratic responses to land-use transformations. We do not cover pollinator restorations within agricultural systems, as these are typically small (<1 ha) in scale and do not represent what is generally meant by land-use change. Pollinator response to such restorations has recently been reviewed elsewhere (Winfree 2010). Studies of the reproduction of animal-pollinated plants as a function of land use are not covered here; they have recently been reviewed elsewhere (Aguilar et al. 2006).

The habitat affinity of most pollinator species is unknown; thus, in this review, we do not refer to habitat loss or fragmentation, but only to transitions between land-use types or land-use change. We standardized land use to multiple natural/seminatural and anthropogenic types (**Figure 2**). We consider these groupings to be crude; in particular, few researchers of landscape-scale studies quantitatively report the composition of the modified, matrix habitats, yet these must be categorized in order to compare the original with the converted type. Even crude habitat categorizations,

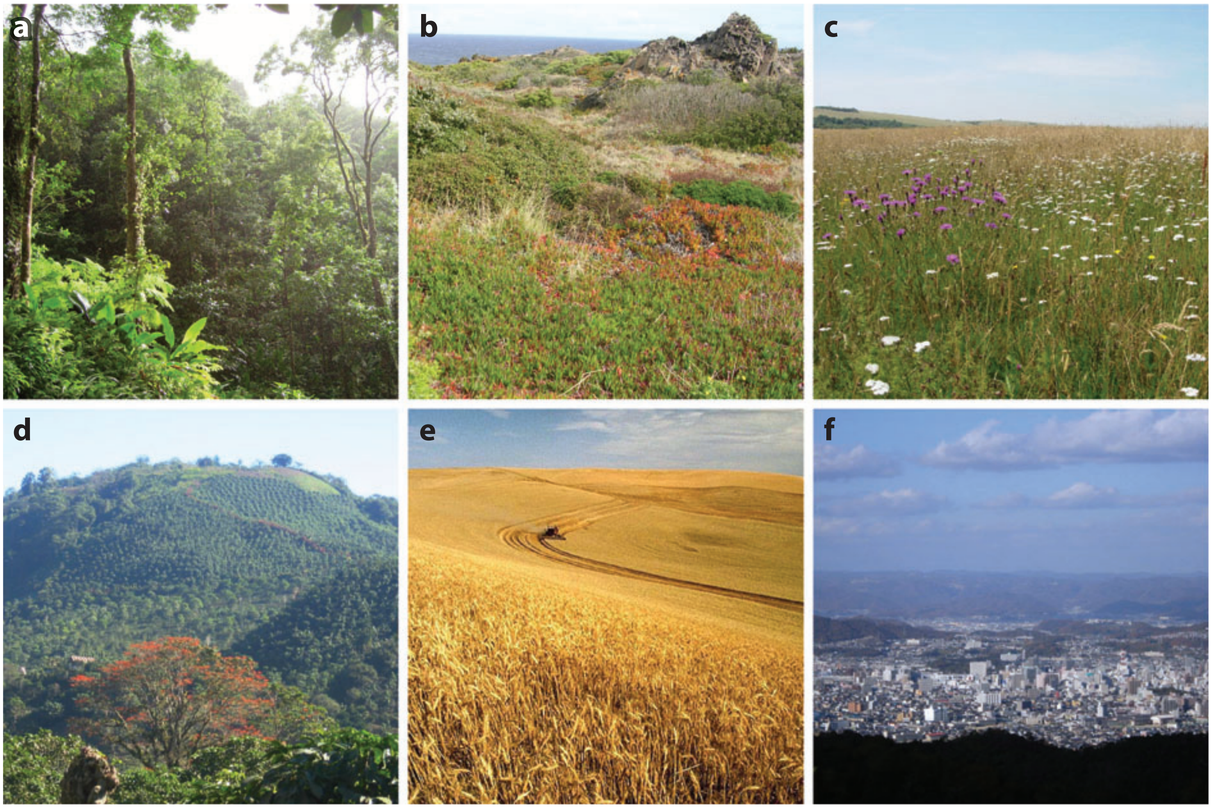

Figure 2

(*Top row*) Representative natural and seminatural habitats: (*a*) tropical forest in Martinica (tropical forest category), (*b*) shrublands (shrub/heath/open woodlands category) in Spain, and (*c*) fallow agriculture (seminatural category) in the United Kingdom. (*Bottom row*) Representative anthropogenic habitats: (*d*) coffee plantation (agriculture category) in Costa Rica, (*e*) wheat (agriculture category) in the United States, and (*f*) urban development (urban/suburban category) in Japan. Additional natural land-use categories that were used, but are not shown here, include temperate forest, desert, and natural grasslands, and for anthropogenic habitats, pasture and deforestation/secondary forest/agroforestry. Photo credits: I. Bartomeus and the following Wikimedia commons and NBII LIFE authors: J. Oliveira, D. VanDerMade, Lanbea, Frameme, and Lizzie.

however, allow for a preliminary exploration of the role of habitat type in determining pollinator responses to land-use change.

In the following sections, we investigate whether the observed variability in pollinator responses to land-use change (**Table 1**) is explained by characteristics of land-use change, by characteristics of the pollinators themselves, or by aspects of research methodology. Because 83% of the recorded pollinator responses are of aggregate pollinator abundance or species richness, we report only these metrics in **Supplemental Tables 2–12** to make comparisons more consistent. In interpreting **Supplemental Tables 2–12**, we focus on the ratio of negative-to-positive responses to reduce the role of variation in statistical power in determining outcomes. We note, however, that nonsignificant or neutral responses are the most frequent response observed (**Table 1**).

Supplemental Material

4. CHARACTERISTICS OF LAND-USE CHANGE

Land-use change processes are complex, and pollinator responses might be conditioned by the type and extent of land-use change. The strongest pattern we find in this section is that pollinator responses vary according to study design, being largely negative in comparisons across gradients in surrounding landscape cover and largely positive in comparisons across local land-use types. In addition, pollinator responses are more strongly negative in study systems that have already experienced extreme land-use change. Pollinators respond more consistently to changes in floral resources than they do to changes in land use per se; thus, floral resources may be a mechanism explaining some of the diversity of pollinator responses to land-use change. The effect of land-use change on other resources required by pollinators, such as nesting sites, has scarcely been investigated.

4.1. Study Design and the Extent of Land-Use Change

Most studies of pollinator response to land-use change use one of two study designs. In the first design, pollinator populations within a fixed habitat type are compared across landscape contexts that differ in the extent of land-use change. In the second design, pollinator populations are compared across habitat types, generally without reference to the land-use composition of the surrounding landscape (**Figure 3**).

We used studies of the first design to investigate how the extent of land-use change affects pollinator outcomes by comparing results from studies performed in systems characterized by extreme human land use to results from systems characterized by only moderate human land use. We categorized studies as extreme versus moderate according to the values they reported for any of the following metrics: the proportion of land cover surrounding the study site that consists of natural habitat (57% of responses); the linear distance to the nearest natural habitat (25% of responses); or the size of the natural habitat fragment where data were collected (17% of responses). Although these metrics are distinguished in the literature on habitat fragmentation and in principle do not have to be positively correlated, in practice species tend to respond to them similarly (Fahrig 2003). To categorize studies, we used the same scheme as a recent meta-analysis of land use and bees (Winfree et al. 2009), which considered studies as being from extreme systems if the most extreme site in the analysis had $\leq$5% natural habitat cover remaining in the surrounding landscape, was $\geq$1 km from the nearest natural habitat, or was a $\leq$1-ha habitat fragment, whereas all other studies were classified as moderate. Winfree et al. (2009) found a highly significant difference in pollinator responses between the extreme and moderate systems, with significant negative responses being found only in extreme systems (**Figure 4**).

Here, we found a similar result using a much larger number of responses [158 responses for bees and butterflies combined versus 81 responses of bees alone (reported in Winfree et al. 2009;

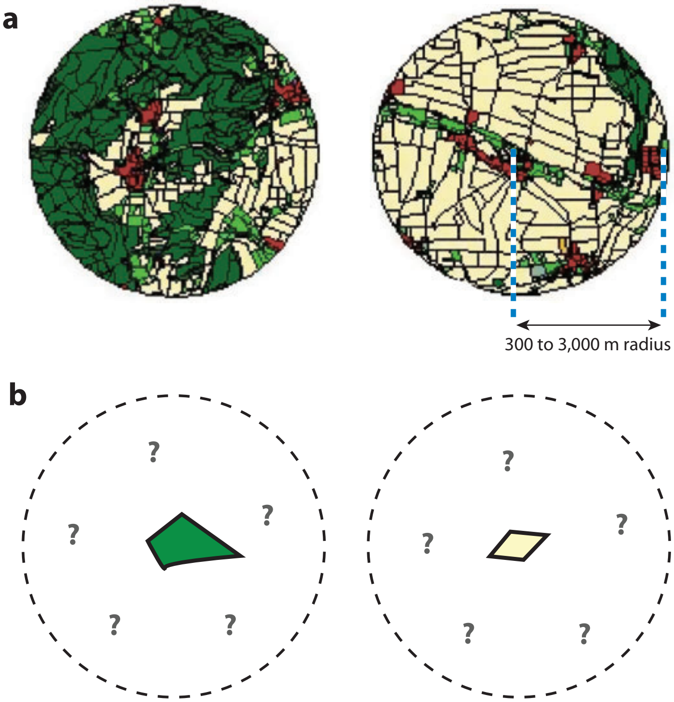

Figure 3

Schematic showing the two study designs contrasted in this review. (*a*) Design focused on surrounding landscape cover. Sampling is generally done within a fixed habitat type. In the most common design, sites vary in the proportion of surrounding land cover composed of specific habitat types such as forest (*dark green*) or agriculture (*yellow*). The radius at which landscape cover is assessed varies across studies but is typically between 300 and 3,000 m. Other designs, which we include in this category, vary either the linear distance to the nearest habitat patch or the area of the habitat patch. (*b*) Design focused on local land-use type. These studies compare pollinator communities among different habitat types. The surrounding landscape cover and the spatial extent of the habitat type where pollinators are sampled are generally not reported.

Figure 4)]. Bees and butterflies both show strong negative responses to land-use change in extreme systems, but more mixed responses in moderate systems (**Supplemental Tables 2** and **3**). Extreme land use causes a strong decrease in abundance and/or richness (e.g., Aizen & Feinsinger 1994, Koh & Sodhi 2004, Kremen et al. 2002, Ockinger & Smith 2006), whereas studies in moderately anthropogenic landscapes find more varied responses (e.g., Bartomeus et al. 2010, Bergman et al. 2008).

Study designs that make comparisons across habitat types, rather than across landscape gradients, find even fewer negative effects, and responses are predominantly positive for most taxa (**Supplemental Table 4**). For bees, the ratio of negative-to-positive responses decreases from 8.2 for extreme landscape studies to 2.0 for moderate landscape studies, to 0.5 for across-habitat comparisons. For butterflies, the ratios decrease from 6.0 to 3.0 to 1.1, respectively (**Supplemental Tables 2–4**). The responses of syrphid flies and vertebrates are difficult to interpret due to the limited number of landscape-scale studies that have been conducted (**Supplemental Tables 2** and **3**).

The reason why pollinator abundance and/or richness often decrease with increasing human land use in the surrounding landscape, but increase with conversion of natural to anthropogenic

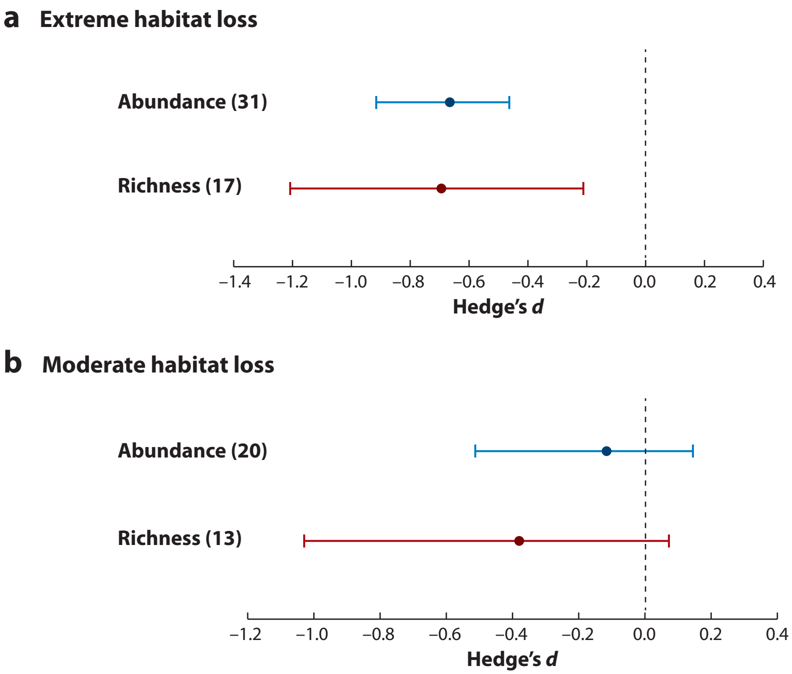

Figure 4

A meta-analysis of bee responses to land use. Weighted-mean effect sizes for changes in bee abundance and species richness in study systems where land use was (*a*) extreme (≤5% natural habitat cover remaining in the surrounding landscape, ≥1 km to the nearest natural habitat, or ≤1-ha habitat fragment) and (*b*) moderate (all other studies not classified as extreme). The effect size, Hedge's *d*, can be interpreted as the inverse-variance-weighted difference in abundance or richness of bees between natural and disturbed conditions, measured in units of standard deviations (Gurevitch & Hedges 2001). Positive values of *d* imply positive effects of anthropogenic disturbance on bees, whereas negative *d* values imply negative effects. Error bars are 95% confidence intervals. Sample sizes are given in parentheses. Modified from Winfree et al. (2009).

habitat types, is difficult to discern using only the information reported in the published literature. In particular, studies comparing across local land-use types rarely report the composition of the surrounding landscape, thus leaving this variable uncontrolled. However, it seems probable that the comparisons across local land-use types are, on average, studying land-use change at a smaller spatial scale than are the comparisons across gradients in surrounding land cover. If this is the case, then pollinators appear to respond increasingly negatively as both the spatial scale and extent of land-use conversion increase. It is difficult to generalize on this point because the few studies that have been designed to explicitly compare the relative effects of local habitat type conversion with land-use change in the surrounding landscape have found mixed effects (Gabriel et al. 2010, Haenke et al. 2009, Holzschuh et al. 2010, Koh & Sodhi 2004, Williams & Kremen 2007). Furthermore, most of these studies contrasted organic versus conventional agriculture locally rather than comparing natural to anthropogenic habitat types. Lastly, a related design has been used in the context of pollinator restorations to investigate the effectiveness of small-scale habitat restorations in different landscape contexts. These studies find an interaction between the local and the landscape scales, such that the transition from locally unrestored to restored habitat results in greater biodiversity benefits in intensively human-used landscapes (reviewed in Winfree 2010), as originally hypothesized by Tscharntke et al. (2005).

4.2. Habitat Type

Specialist species: species requiring particular habitat conditions or resources

Biotic homogenization: an increase in the taxonomic similarity of biotas over time

The term land-use change encompasses a wide variety of actual habitat transitions, but in general it creates more open or early successional habitats. This leads to the prediction that at least some pollinator taxa will respond positively to land-use change. For example, although forest-specialist bee species exist, bees in general are considered creatures of open habitats (Michener 2007, p. 4). Likewise, in the temperate zone butterflies tend to be associated with open areas, although this is less true in the tropics (Scoble 1995). Syrphid flies are often more abundant, and in some systems more diverse, in open areas (Deans et al. 2007). We predicted that the type of habitats transitioned to and from might be an important determinant of pollinator responses to land-use change with, for example, forest-to-open transitions having different effects from open-to-open transitions. In an analogous way, habitat identity mitigates the responses of multiple taxa to habitat edges (Ries et al. 2004). Although overall the number of published studies is not sufficient to draw conclusions regarding all specific pairwise transitions (**Supplemental Tables 5–7**), two patterns do emerge.

First, in comparisons across habitat types, pollinator abundance and/or species richness are often lower in forests as compared to more open, anthropogenic habitats (**Supplemental Table 7**). Tropical birds and bats, in particular, appear to benefit from agroforestry or logging in many cases (Tscharntke et al. 2008, Willig et al. 2007). An important caveat, however, is that the literature is dominated by studies of aggregate abundance and species richness, and these metrics would not reveal changes in composition such as replacement of forest specialist species with common generalist species (Tylianakis et al. 2005).

Second, many studies use moderately anthropogenic habitats such as grazed grasslands, fallow agriculture, and suburban gardens as the focal, good pollinator habitat. These seminatural habitats are then compared to more intensive land use. In addition, some analyses combine native vegetation (generally forest) with intensive anthropogenic land-use categories for analysis (e.g., Steffan-Dewenter et al. 2002). Most of these studies find that the loss of seminatural habitats has negative effects on pollinators of various taxa (Kleijn & van Langevelde 2006, Krauss et al. 2009, Krauss & Steffan-Dewenter 2003, Sjodin et al. 2008; see **Supplemental Tables 5–7**). This body of work provides additional support for the hypothesis that moderate human land use is compatible with the persistence of at least some pollinators (see sidebar, Habitat Heterogeneity, Common Species, and Biotic Homogenization).

Supplemental Material

Rigorous comparisons of pollinator responses according to the type of anthropogenic habitat transitioned to are not possible, because few habitat types other than agriculture have been investigated (**Supplemental Tables 8–10**). The predominance of agriculture in the published literature is representative of global land-use patterns, insofar as agriculture accounts for 38% of ice-free terrestrial land area worldwide, whereas urban/suburban settlements account for only 8% (Ellis et al. 2010). However, it leaves a research gap regarding pollinator responses to other types of land-use transitions. For example, butterflies may be particularly negatively affected by urbanization, but small sample sizes make this conclusion tentative (**Supplemental Tables 8** and **10**).

4.3. Floral Resources as a Mechanism Underlying Responses to Land-Use Change

Although pollinators can diverge widely in life-history traits, they share a reliance on flowers as a food source. Floral resources can be a limiting factor for populations of bees (Roulston & Goodell 2011), Lepidoptera (Ockinger & Smith 2006, Summerville & Crist 2001), syrphid flies (Kleijn & van Langevelde 2006, Meyer et al. 2009), birds (Lara 2006), and bats (Tschapka 2004). The published studies that report quantitative measures for all three variables—land-use change, floral density, and pollinator responses—suggest that pollinator responses track floral resources

HABITAT HETEROGENEITY, COMMON SPECIES, AND BIOTIC HOMOGENIZATION

Some studies find that moderate land use maximizes the richness and abundance of pollinators, including butterflies (Blair 1999, Hogsden & Hutchinson 2004), bees (Kessler et al. 2009), and birds (Tscharntke et al. 2008). Low-level anthropogenic land use may increase heterogeneity of habitats and resources, thus increasing niche diversity (Tews et al. 2004). For example, pollinators could nest in forest habitats but forage in agricultural habitats (Klein et al. 2003). Consistent with this hypothesis, edges between different land-use types often show the highest diversity of butterflies and bees (Brosi 2009, Hagen & Kraemer 2010, Ohwaki et al. 2007, Vu 2009). However, this pattern may be driven by common species, thus masking effects on rare species and leading to homogenization on larger scales. More studies of pollinator community composition are needed in order to determine whether biotic homogenization is occurring. A related situation arises in a restoration context through agricultural policies that create pollinator habitat on agricultural lands. Such programs may primarily benefit common species, which can persist in agricultural landscapes (Kleijn et al. 2006). Such programs may even contribute to the decline of more vulnerable species elsewhere if additional lands are converted to agriculture to make up production shortfalls (Hodgson et al. 2010). Thus studies of species composition are needed in this context as well.

regardless of its directionality with land-use change. When floral resources decrease with land-use change, pollinators decrease as well, whereas when floral resources increase with land-use change, so do pollinators (see **Supplemental Table 11**).

4.4. Other Mechanistic Factors

A true predictive understanding of pollinators and land-use change would be based on knowledge of the mechanistic factors that underlie pollinator response to each type of habitat type conversion. However, mechanistic factors other than floral resources have rarely been measured for pollinators in the context of land-use change. In particular, nest or oviposition site availability might be important, but has scarcely been measured. Among bees, species nesting in existing cavities above ground decrease with increasing land-use change (Williams et al. 2010), suggesting that these nest sites are destroyed when habitats are converted. Conversely, bee species that nest in the ground increase with land-use change (Williams et al. 2010), possibly because human activities improve access to bare soil. For butterflies, mowing or grazing may have detrimental effects if it destroys the plants on which females have oviposited (Johst et al. 2006). Nest site selection and success in birds are often tied to vegetation structure, which clearly can change with land use (Smith et al. 2009); however, we are not aware of studies investigating land-use change and nest selection for pollinating birds. Some nectarivorous bats use tree hollows as roost sites, and these can be destroyed by logging (Law 1993).

5. CHARACTERISTICS OF POLLINATORS

The broad groups of pollinators (bees, butterflies, flies, and vertebrates) do not show markedly different responses to land-use change once study design is taken into account. Across taxa, the species trait that is most often associated with vulnerability to land-use change is dietary specialization, with pollen-specialist bees, and fly and butterfly larval-host specialists, being the most sensitive. Within each taxon, other biological differences among species explain some variability, with nest site location and sociality being important in bees and mobility being important in syrphid flies and butterflies.

5.1. Are There Broad Differences Across Pollinator Taxa?

As far as we are aware, differential responses to land-use change among the primary pollinator taxa have never been evaluated. There are multiple ecological differences across these groups that might lead to differential responses to land-use change. Perhaps the most obvious is body size, contrasting the insects with the mammals. However, predictions about response to land-use change based on body size are difficult to make, due not only to a multiplicity of other factors that vary between these groups, but also to contrasting expectations with regards to the effect of body size. Small-bodied pollinators such as insects might require smaller areas in order to achieve minimum viable population sizes, thus making them less sensitive to land-use change (Tscharntke et al. 2002). Conversely, larger-bodied and therefore more mobile pollinators might be better able to find resources throughout the landscape (Henle et al. 2004). When broad comparisons are made across taxa using the ratio of negative-to-positive responses, without controlling for study design, bees and butterflies appear to be the most sensitive to land-use change, whereas vertebrates are the least sensitive (**Table 1**). However, a closer examination reveals that 80% of vertebrate studies have used a study design that compares across local land-use types, and such designs find fewer negative responses to land-use change regardless of taxon (**Figure 3**; **Supplemental Tables 2–4**). When comparisons across taxa are made only within this study design, few differences emerge across taxa (**Supplemental Table 4**). Similarly, studies that have investigated the responses of multiple taxonomic groups within the same system have not found stark differences (**Supplemental Table 12**). However, a meta-analysis focused exclusively on tropical systems found that bees were negatively affected by conversion to agroforestry, whereas nectarivorous birds benefited from moderate levels of agroforestry (Tscharntke et al. 2008).

Supplemental Material

5.2. Do Species Traits Explain Variation within Each Taxonomic Group?

Within each broad taxonomic group, species traits such as dietary or habitat specialization, nesting requirements, body size, or sociality might mediate responses to land-use change. These traits can have somewhat different meanings across the main groups of pollinators. For example, dietary specialization in bees, or oligolecty, refers to species for which females collect pollen only from one to a few genera or families of plants. In contrast, with a few notable exceptions such as yucca moths, adult Lepidoptera and syrphid flies show little flower specialization, visiting mainly open flowers with abundant nectar reward (Scoble 1995). Dietary specialization in butterflies and syrphid flies thus refers not to adults, but to the breadth of host plants or prey items that the larvae feed upon. In contrast to pollen specialization, nectar specialization is rare; thus, adult pollinators that feed upon nectar alone, such as male bees, most butterflies, and vertebrates, are mostly generalists (Michener 2007, Scoble 1995). Many nectarivorous bird and bat species are even more generalist than the generalist insects, because they can forage on fruit or insects when nectar is not available (Tschapka 2004).

The definition of nesting resources also varies across taxa. Syrphid flies and butterflies do not have nests, but host specialists require particular plants for oviposition, or particular prey species. Birds and bees both show wide variation across species in the resources they require for nesting, ranging from use of certain types of preexisting cavities to particular plant species required as nest-building materials. A number of nectarivorous bats use caves for roosts that may be susceptible to anthropogenic activity. Lastly, the species trait of sociality applies primarily to bees, for which roughly 6% of species are social (Michener 2007); the other pollinator taxa have few or no social species.

In bees, a synthetic analysis of 19 data sets shows that nest location (discussed in Section 4.4 above) and sociality are the most important traits moderating response to land-use change

(Williams et al. 2010). Several recent meta-analyses have found that social bees are more negatively affected by land-use change than are solitary species (Ricketts et al. 2008, Williams et al. 2010, Winfree et al. 2009). Although the mechanism behind this effect is unknown, one hypothesis is that pesticides bio-accumulate in the larger and more persistent nests of social species, thereby increasing exposure at all life-history stages (Williams et al. 2010). Neither dietary (floral) specialization nor body size predicts responses to isolation from natural habitat in a synthetic analysis (Williams et al. 2010), despite the fact that some work has found that floral specialist bees decline more with land-use change (Biesmeijer et al. 2006, Cane et al. 2006, Kleijn & Raemakers 2008).

In butterflies and moths, a cross-continental analysis of 24 data sets found that species with specialized larval diets, low mobility, and low reproduction are the most strongly affected by land use (Ockinger et al. 2010). This result concurs with an independent analysis of the ecological characteristics of threatened butterflies (Kotiaho et al. 2005). First, the idea that dietary specialist species are the first to disappear is highly supported by multiple studies in different systems across the world (Filippi-Codaccioni et al. 2010, Koh & Sodhi 2004, Littlewood 2008, Polus et al. 2007, Stefanescu et al. 2009, Steffan-Dewenter & Tscharntke 2000; **Figure 5**). Second, low mobility, measured as wing size, is also associated with negative responses, although this trend is more pronounced in moths than in butterflies (Ockinger et al. 2010). This finding supports the idea that, at least among Lepidoptera, more mobile organisms are better able to disperse and find suitable habitat patches. Third, high reproductive rate can mitigate the negative effects of land use on highly specialist species (Ockinger et al. 2010), and species with few generations per year are absent from human habitats in some systems (Kitahara & Sei 2001). Lastly, endemics and species with small ranges are most sensitive to land-use change (Bonebrake et al. 2010, Kitahara & Sei 2001).

As in butterflies, larval food source is an important determinant of syrphid fly response to land-use change, with more generalist species being more resilient (Schweiger et al. 2007). In particular, syrphid flies that consume aphids increase in agricultural settings, whereas some phytophagous and saprophagous species decrease (Meyer et al. 2009, Schweiger et al. 2007). Syrphid flies with greater mobility are less susceptible to land-use changes (Schweiger et al. 2007, Sommaggio 1999).

We know of no studies that have examined the relationship between species-level traits of flower-visiting vertebrates and the response to land-use change. In fact, feeding guild itself is an important trait determining bird and bat responses to land use, with nectarivorous species being more resilient to land-use change, as compared to other feeding guilds (Tscharntke et al. 2008, Willig et al. 2007).

6. RESEARCH METHODS AND BIASES

In this section, we review methodological issues relevant to the interpretation of the literature on pollinators and land use. First, most published studies report species richness and/or aggregate abundance as the outcome variables. More studies of species composition are needed in order to detect changes such as trade-offs between disturbance-sensitive and disturbance-associated species. If such trade-offs occur they could lead to biotic homogenization at larger scales (Olden 2006). Second, land-use change is usually studied by comparing habitats across space, whereas studies of land-use change over time are scarce. Although the results of studies using space as opposed to time designs do not appear to differ at present, more studies over time are needed. Third, the contrasting results found by studies using different spatial designs (discussed in Section 4 above) raise scope of inference issues. In addition, most of the published studies investigating changes in pollinator communities along land-use gradients have been done in systems characterized by extreme human land use. This may not represent a random sample, with respect to land-use change, of all global ecosystems.

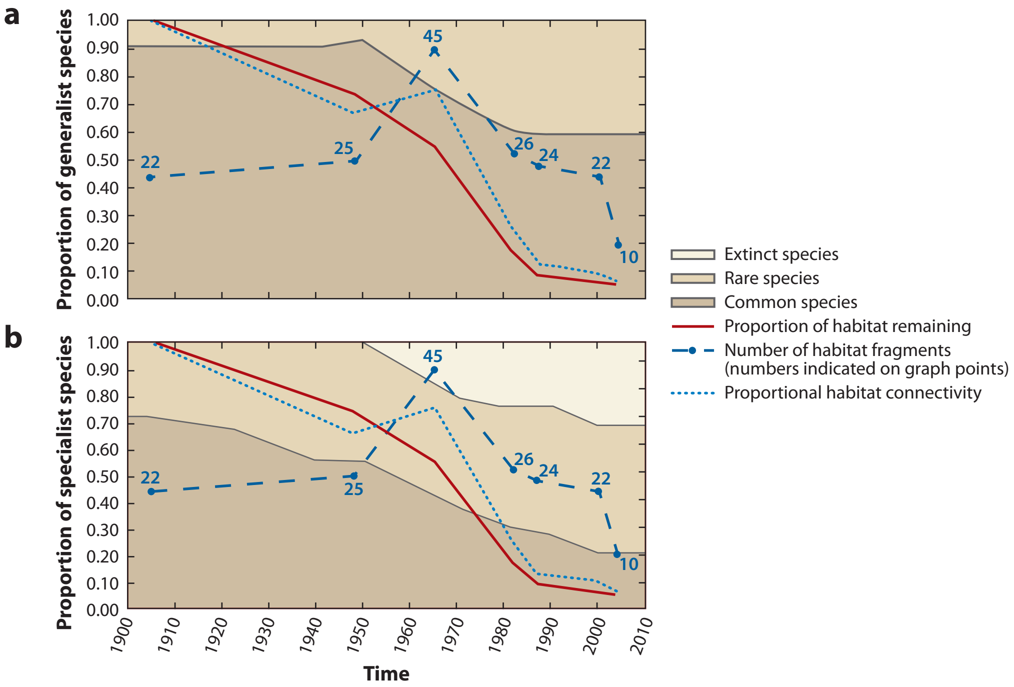

Figure 5

Changes in butterfly communities over time in southern Belgium, illustrating three important issues. First, this is one of the few long-term studies available, and it indicates than many changes took place before the majority of studies covered in this review were initiated. Second, it demonstrates the importance of using community composition rather than simpler metrics such as species richness, which do not capture the trade-offs among rare and common species captured here. Third, the data show the greater susceptibility of specialist species. The graphs show changes within (*a*) generalist or (*b*) specialist butterfly communities since 1903. The proportions of common, rare, and extinct species change over time. Superimposed, the remaining area of calcareous grassland habitat (*solid red line*), the number of habitat fragments (*dashed line*), and the connectivity among these (*dotted line*) show the association between land-use change and species composition. Modified from Polus et al. 2007.

6.1. Response Variables

In this section we consider the frequency with which various measures have been used to represent pollinator response to land-use change and how the choice of response variables may influence the conclusions reached. We highlight the lack of studies of species composition, which severely limits our understanding of pollinators and land-use change thus far.

6.1.1. Does species composition change more than abundance and richness? Richness and abundance are simple indices that are useful in evaluating large-scale trends, but they can mask changes in the identity or composition of species, and such changes may be the main result of anthropogenic land use (Barlow et al. 2007, Lewis 2009). When composition changes more than abundance and richness, this implies that some species increase with land-use change while others decrease. Such changes can lead to biotic homogenization if the subset of species that persist in anthropogenic habitats become widespread at the expense of species adapted to particular natural habitat types.

Few studies of bees report community composition, but those that do find it to be more sensitive to land-use change than are abundance and richness (Brosi et al. 2007, Hannon & Sisk 2009). A

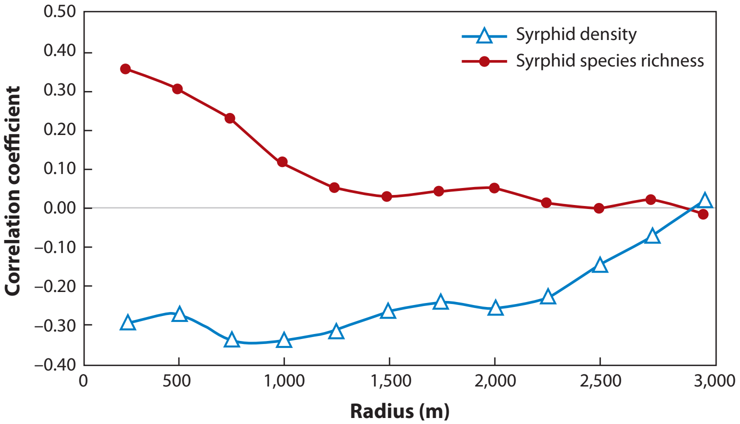

Figure 6

Contrasting responses of richness and abundance to land-use change. Each point represents the correlation between landscape diversity (which is negatively associated with arable land cover in this system) and either syrphid fly abundance or richness at each radius (meters). Adapted from Meyer et al. (2009).

repeated finding in bee communities is that native species decrease and feral honey bees (*Apis mellifera*) increase with increasing land-use change (Aizen & Feinsinger 1994, Brosi et al. 2008). In butterfly studies, composition is more often reported, and it is consistently more sensitive to land use than are richness and abundance. However, the precise pattern of change varies among studies. In some cases, composition changes mainly due to the loss of particular species from the more anthropogenic habitats, such that composition is nested (Ockinger & Smith 2006). Even in the opposite case, in which natural habitats have lower richness, the natural habitats can support species not found elsewhere, thus indicating the importance of the natural habitat type (Natuhara et al. 1999, Spitzer et al. 1993). A third pattern shows similar richness in both land-use types, but with widely divergent community composition (Ohwaki et al. 2007, Summerville & Crist 2003). In such cases, composition effects can be driven by the presence of widespread generalist species in more anthropogenic habitats, accompanied by the loss of specialist species (Balmer & Erhardt 2000, Stefanescu et al. 2005).

Most studies on syrphid flies are conducted across agricultural land-use gradients, and forest-associated and phytophagous species are often absent from the most agricultural sites, leading to decreases in species richness with increasing land-use change (Meyer et al. 2009, Schweiger et al. 2007). At the same time, the smaller number of species whose larvae consume aphids or other crop pests often increase with agriculture, leading to stable or even increasing abundance with land-use change (Meyer et al. 2009; **Figure 6**). All of this work suggests that the focus on abundance and richness is too simplistic and misses important patterns, such as the replacement of forest-dependent species with disturbance-associated species.

6.1.2. Reproduction as an outcome variable. Outcome variables related to population growth rate, such as reproductive success or nest density, would be very useful in predicting the effects of land-use change on pollinators. Unfortunately, these variables have rarely been reported, probably because they are difficult to measure. The few studies of bee nesting or reproduction as a function of land use show mixed effects (Goulson et al. 2010, Holzschuh et al. 2010, Williams & Kremen 2007). We were unable to find quantitative studies of butterfly or fly reproductive success as a function of land-use change, probably because the lack of a central nest site complicates the monitoring of such variables.

6.2. Issues of Space and Time

Most studies of land-use change are conceptually focused on land-use transitions—that is, changes in land use over time—but in practice collect data simultaneously in land-use contexts, thus substituting space for time. Because the assumptions of this substitution are rarely validated, it is worth asking whether designs based on time achieve results similar to those based on space. Few studies have used an across-time design, but those that do have found results broadly consistent with the across-space designs. For example, among butterflies, extinctions occur mainly in specialist species over time (Nilsson et al. 2008, Ohwaki et al. 2008, Polus et al. 2007, Stefanescu et al. 2009). In a tropical forest fragmentation experiment, hummingbird species either remained stable or increased following deforestation, and they remained stable for the following 20 years (Stouffer et al. 2006). This is consistent with the largely neutral-to-positive responses of nectarivores to tropical forest loss generally (Tscharntke et al. 2008).

A related concept, which can be investigated using either time or space designs, is time-delayed extinctions or extinction debt. Among bees, extinction debt has been found for particular floral specialists but not for other taxa (Cane et al. 2006). A pan-European study of 147 fragmented grassland remnants found support for the extinction debt hypothesis for vascular plants, but not for specialist butterflies (Krauss et al. 2010). However, in a similar study system, butterfly species requiring large habitat areas do show signs of extinction debt (Sang et al. 2010).

A final issue related to historical land-use transitions is that they can act as a filter on pollinator communities, which may now be dominated by species that are relatively robust to human land use. Thus, contemporary studies finding little effect of land-use change may be biased insofar as the sensitive species were lost before the studies were conducted (**Figure 5**).

6.3. Scope of Inference

Supplemental Material

The scope of inference for published studies of pollinators and land-use change will be global in scope only if the systems that have been studied thus far represent a globally random sample with respect to land use. We can use the published studies of pollinators and surrounding land use (**Supplemental Tables 2–3**) to do a preliminary assessment of this issue. Using the criteria for an extremely anthropogenic system described in Section 4 above, 75% of bee studies, 55% of butterfly studies, 84% of fly studies, and 45% of vertebrate studies have been conducted in extremely anthropogenic systems. Thus, a research bias may exist wherein researchers have chosen to study pollinators and land-use change in systems that have already experienced greater than average land conversion. Conversely, a research bias may exist in the opposite direction if researchers have chosen systems where they expect to find sufficient numbers of native pollinators to study and these systems have less land conversion than average. This bias would lead to an underestimate of the actual global effects of land-use change on pollinators. Robust inferences about the effects of land-use change on pollinators globally will need to take into account the actual distribution of anthropogenic and natural systems, as compared to the systems where pollinators have been studied.

SUMMARY POINTS

1. Pollinator responses to land-use change are more often negative than positive, but are characterized by high variability.

2. Pollinator responses vary according to study design, being largely negative in comparisons across gradients in surrounding landscape cover and largely positive in comparisons across local land-use types. In addition, pollinator responses are more strongly negative in study systems that have already experienced extreme land-use change.
3. Pollinators respond more consistently to the directionality of change in floral resources with land-use change than they do to land-use change itself.
4. The most prominent trait associated with vulnerability to land-use change across taxa is dietary specialization, with pollen specialist bees, and fly and butterfly larval host specialists, being most sensitive.
5. Conclusions thus far are largely based on measures of aggregate abundance and species richness. More studies of species composition and relative abundance are needed in order to understand which pollinators are lost and gained with land-use change.

FUTURE ISSUES

Gaps in knowledge resulting from research bias:

1. Are the systems in which pollinators and land use have been studied a random sample of all global systems, with respect to land use? The answer determines the appropriate scope of inference for the published literature.
2. What is the role of extinction debt in explaining long-term changes in pollinator communities? A time lag can exist between land use and the loss of native species, yet very few studies of pollinators have considered time since land-use change took place. A related bias is that the historical baseline for what species were present before any land-use change took place is rarely known, thus potentially biasing contemporary studies if sensitive species are no longer present.

Moving beyond species richness:

3. How does pollinator species composition change with land use? Are disturbance-sensitive species replaced with disturbance-associated species, leading to biotic homogenization? As of yet, the great majority of studies have focused on aggregate abundance and species richness alone, leaving these questions largely unexplored.

Identifying mechanisms:

4. What are the mechanisms underlying pollinator responses to land-use change? Mechanisms other than floral resources have scarcely been investigated.

Future scenarios:

5. How are future trends in land use likely to affect pollinators? Agricultural land area in particular is predicted to increase greatly with the increasing human population (Tilman et al. 2001). What are the trade-offs for pollinators between intensifying agriculture within existing agricultural areas (the land sparing approach) and using larger areas in a more biodiversity-compatible way (the wildlife-friendly farming approach; Hodgson et al. 2010)? What interactions might there be between land use and climate change (Forister et al. 2010)?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Jason Tylianakis, Leslie Ries, David Pattemore, David Wilcove, Neal M. Williams, Tina Harrison, Faye Benjamin, and Molly MacLeod for improving the manuscript with their comments. I.B. was funded by a Postdoctoral Fellowship from the Spanish Education Ministry (ref: EX2009-1017).

This paper is dedicated to Joan Ehrenfeld, scientist, mentor, and friend, who died far too young between the initiation and publication of this paper.

LITERATURE CITED

Aguilar R, Ashworth L, Galetto L, Aizen M. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9:968–80

Aizen MA, Feinsinger P. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "chaco serrano." *Ecol. Appl.* 4:378–92

Balmer O, Erhardt A. 2000. Consequences of succession on extensively grazed grasslands for Central European butterfly communities: rethinking conservation practices. *Conserv. Biol.* 14:746–57

Barlow J, Gardner TA, Araujo IS, Ávila-Pires TC, Bonaldo AB, et al. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. USA* 104:18555–60

One of few experimental studies, and one of the few to examine community composition.

Bartomeus I, Vila M, Steffan-Dewenter I. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J. Ecol.* 98:440–50

Bergman K-O, Ask L, Askling J, Ignell H, Wahlman H, Milberg P. 2008. Importance of boreal grasslands in Sweden for butterfly diversity and effects of local and landscape habitat factors. *Biodivers. Conserv.* 17:139–53

Bernhardt P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms. *Plant Syst. Evol.* 222:293–320

Biesmeijer JC, Roberts SPM, Reemer M, Oholemuller R, Edwards M, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–54

Blair RB. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecol. Appl.* 9:164–70

Bonebrake TC, Ponisio LC, Boggs CL, Ehrlich PR. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. *Biol. Conserv.* 143:1831–41

Brosi BJ. 2009. The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini). *Biol. Conserv.* 142:414–23

Brosi BJ, Daily GC, Ehrlich PR. 2007. Bee community shifts with landscape context in a tropical countryside. *Ecol. Appl.* 17:418–30

Brosi BJ, Daily GC, Shih TM, Oviedo F, Duran G. 2008. The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* 45:773–83

Cane JH, Minckley R, Kervin L, Roulston T, Williams N. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol. Appl.* 16:632–44

Carthew SM, Goldingay RL. 1997. Non-flying mammals as pollinators. *Trends Ecol. Evol.* 12:104–8

Deans AM, Smith SM, Malcolm JR, Crins WJ, Bellocq MI. 2007. Hoverfly (Syrphidae) communities respond to varying structural retention after harvesting in Canadian peatland black spruce forests. *Environ. Entomol.* 36:308–18

Elberling H, Olesen JM. 1999. The structure of a high latitude plant-flower visitor system: the dominance of flies. *Ecography* 22:314–23

Ellis EC, Goldewijk KK, Siebert S, Lightman D, Ramankutty N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecol. Biogeogr.* 19:589–606

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34:487–515

Filippi-Codaccioni O, Devictor V, Bas Y, Julliard R. 2010. Toward more concern for specialisation and less for species diversity in conserving farmland biodiversity. *Biol. Conserv.* 143:1493–500

Fleming TH, Geiselman C, Kress WJ. 2009. The evolution of bat pollination: a phylogenetic perspective. *Ann. Bot.* 104:1017–43

Fleming TH, Muchhala N. 2008. Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *J. Biogeogr.* 35:764–80

Forister ML, McCall AC, Sanders NJ, Fordyce JA, Thorne JH, et al. 2010. Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proc. Natl. Acad. Sci. USA* 107:2088–92

Gabriel D, Sait SM, Hodgson JA, Schmutz U, Kunin WE, Benton TG. 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecol. Lett.* 13:858–69

Goulson D, Lepais O, O'Connor S, Osborne JL, Sanderson RA, et al. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. *J. Appl. Ecol.* 47:1207–15

Gurevitch J, Hedges VL. 2001. Meta-analysis: combining the results of independent experiments. In *Design and Analysis of Ecological Experiments*, ed. SM Scheiner, J Gurevitch, pp. 347–69. New York: Oxford Univ. Press

Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C. 2009. Increasing syrphid fly diversity and density in sown flower strips within simple versus complex landscapes. *J. Appl. Ecol.* 46:1106–14

Hagen M, Kraemer M. 2010. Agricultural surroundings support flower-visitor networks in an Afrotropical rain forest. *Biol. Conserv.* 143:1654–63

Hannon LE, Sisk TD. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biol. Conserv.* 142:2140–54

Henle K, Davies KF, Kleyer M, Margules C, Settele J. 2004. Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* 13:207–51

Herrera CM. 1987. Components of pollinator "quality": comparative analysis of a diverse insect assemblage. *Oikos* 50:79–90

Hodgson JA, Kunin WE, Thomas CD, Benton TG, Gabriel D. 2010. Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecol. Lett.* 13:1358–67

Hogsden KL, Hutchinson T. 2004. Butterfly assemblages along a human disturbance gradient in Ontario, Canada. *Can. J. Zool.* 82:739–48

Holzschuh A, Steffan-Dewenter I, Tscharntke T. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J. Anim. Ecol.* 79:491–500

Johst K, Drechsler M, Thomas J, Settele J. 2006. Influence of mowing on the persistence of two endangered large blue butterfly species. *J. Appl. Ecol.* 43:333–42

Kearns CA, Inouye DW, Waser NM. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.* 29:83–112

Kessler M, Abrahamczyk S, Bos M, Buchori D, Putra DD, et al. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. *Ecol. Appl.* 19:2142–56

Kitahara M, Sei K. 2001. A comparison of the diversity and structure of butterfly communities in semi-natural and human-modified grassland habitats at the foot of Mt. Fuji, central Japan. *Biodivers. Conserv.* 10:331–51

Kleijn D, Baquero RA, Clough Y, Diaz M, De Esteban J, et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9:243–54

Kleijn D, Raemakers I. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* 89:1811–23

Kleijn D, van Langevelde F. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic Appl. Ecol.* 7:201–14

Klein AM, Steffan-Dewenter I, Tscharntke T. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. London Ser. B* 270:955–61

Koh LP. 2007. Impacts of land use change on South-east Asian forest butterflies: a review. *J. Appl. Ecol.* 44:703–13

Koh LP, Sodhi NS. 2004. Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecol. Appl.* 14:1695–708

Finds, in one of the first studies to do so, that the effects of land-use change vary by pollinator life history.

Reviews butterfly responses to land-use change in Southeast Asia, an area experiencing rapid development and in need of conservation attention.

Kotiaho JS, Kaitala V, Komonen A, Päivinen J. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proc. Natl. Acad. Sci. USA* 102:1963–67

Krauss J, Alfert T, Steffan-Dewenter I. 2009. Habitat area but not habitat age determines wild bee richness in limestone quarries. *J. Appl. Ecol.* 46:194–202

Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, et al. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* 13:597–605

Krauss J, Steffan-Dewenter I. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *J. Biogeogr.* 30:889–900

Kremen C. 2005. Managing ecosystem services: What do we need to know about their ecology? *Ecol. Lett.* 8:468–79

Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA* 99:16812–16

Demonstrates the negative impacts of agricultural intensification on native bees.

Lara C. 2006. Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. *Ecoscience* 13:23–29

Larson BMH, Kevan PG, Inouye DW. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Can. Entomol.* 133:439–65

Law BS. 1993. Roosting and foraging ecology of the Queensland blossom bat (*Syconycteris australis*) in north-eastern New South Wales: flexibility in response to seasonal variation. *Wildl. Res.* 20:419–31

Lewis OT. 2009. Biodiversity change and ecosystem function in tropical forests. *Basic Appl. Ecol.* 10:97–102

Highlights the importance of studying species composition and function to detect land-use effects.

Littlewood NA. 2008. Grazing impacts on moth diversity and abundance on a Scottish upland estate. *Insect Conserv. Divers.* 1:151–60

Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, et al. 2011. Reconnecting plants and pollinators: challenges in the ecological restoration of pollination mutualisms. *Trends Plant Sci.* 16:4–12

Meyer B, Jauker F, Steffan-Dewenter I. 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.* 10:178–86

Addresses feeding guild responses of syrphid flies to land use and demonstrates that richness and abundance may have different responses.

Michener CD. 2007. *The Bees of the World.* Baltimore, MD: Johns Hopkins Univ. Press. 953 pp. 2nd ed.

Mound LA. 2005. Thysanoptera: diversity and interactions. *Annu. Rev. Entomol.* 50:247–69

Murray TE, Kuhlmann M, Potts SG. 2009. Conservation ecology of bees: populations, species and communities. *Apidologie* 40:211–36

Natl. Res. Counc. 2007. *Status of Pollinators in North America.* Washington, DC: Natl. Acad. Press. 304 pp.

Natuhara Y, Imai C, Takahashi M. 1999. Pattern of land mosaics affecting butterfly assemblage at Mt Ikoma, Osaka, Japan. *Ecol. Res.* 14:105–18

Neff JL, Simpson BB. 1993. Bees, pollination systems and plant diversity. In *Hymenoptera and Biodiversity*, ed. J LaSalle, ID Gauld, pp. 143–67. Wallingford, UK: CAB Int.

Nilsson S, Franzén M, Jönsson E. 2008. Long-term land-use changes and extinction of specialised butterflies. *Insect Conserv. Divers.* 1:197–207

Ockinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol. Lett.* 13:969–79

Highlights the power of using pollinator life-history traits to explain the effects of land-use change on butterflies.

Ockinger E, Smith HG. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* 149:526–34

Ohwaki A, Tanabe S-I, Nakamura K. 2007. Butterfly assemblages in a traditional agricultural landscape: importance of secondary forests for conserving diversity, life history specialists and endemics. *Biodivers. Conserv.* 16:1521–39

Ohwaki A, Tanabe S-I, Nakamura K. 2008. Effects of anthropogenic disturbances on the butterfly assemblage in an urban green area: the changes from 1990 to 2005 in Kanazawa Castle Park, Japan. *Ecol. Res.* 23:697–708

Olden JD. 2006. Biotic homogenization: a new research agenda for conservation biogeography. *J. Biogeogr.* 33:2027–39

Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–26

Patiny S, Rasmont P, Michez D. 2009. A survey and review of the status of wild bees in the West-Palaearctic region. *Apidologie* 40:313–31

Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, et al. 2010. Scenarios for global biodiversity in the 21st century. *Science* 330:1496–501

Polus E, Vandewoestijne S, Choutt J, Baguette M. 2007. Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. *Biodivers. Conserv.* 16:3423–36

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25:345–53

Rathcke BJ, Jules ES. 1993. Habitat fragmentation and plant-pollinator interactions. *Curr. Sci.* 65:273–77

Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, et al. 2008. Landscape effects on crop pollination services: Are there general patterns? *Ecol. Lett.* 11:499–515

Rico-Gray V, Oliveira PS. 2006. *Ecology of Ant-Plant Interactions*. Chicago: Univ. Chicago Press. 331 pp.

Ries L, Fletcher RJ, Battin J, Sisk TD. 2004. Ecological responses to habitat edges: mechanisms, models, and variabilty explained. *Annu. Rev. Ecol. Syst.* 35:491–522

Roulston TH, Goodell K. 2011. The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* 56:293–312

Sahli HF, Conner JK. 2007. Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanismum* (Brassicaceae). *Am. J. Bot.* 94:203–9

Sang A, Teder T, Helm A, Pärtel M. 2010. Indirect evidence for an extinction debt of grassland butterflies half century after habitat loss. *Biol. Conserv.* 143:1405–13

Schweiger O, Musche M, Bailey D, Billeter R, Diekotter T, et al. 2007. Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos* 116:461–72

Scoble J. 1995. *The Lepidoptera: Form, Function and Diversity*. New York: Oxford Univ. Press. 404 pp.

Sjodin NE, Bengtsson J, Ekbom B. 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *J. Appl. Ecol.* 45:763–72

Smith DM, Finch DM, Hawksworth DL. 2009. Black-chinned hummingbird nest-site selection and nest survival in response to fuel reduction in a southwestern riparian forest. *Condor* 111:641–52

Sommaggio D. 1999. Syrphidae: Can they be used as environmental bioindicators? *Agric. Ecosyst. Environ.* 74:343–56

Spitzer K, Novotny V, Tonner M, Leps J. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *J. Biogeogr.* 20:109–21

Stefanescu C, Peñuelas J, Filella I. 2005. Butterflies highlight the conservation value of hay meadows highly threatened by land-use changes in a protected Mediterranean area. *Biol. Conserv.* 126:234–46

Stefanescu C, Peñuelas J, Filella I. 2009. Rapid changes in butterfly communities following the abandonment of grasslands: a case study. *Insect Conserv. Divers.* 2:261–69

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–32

Steffan-Dewenter I, Tscharntke T. 2000. Butterfly community structure in fragmented habitats. *Ecol. Lett.* 3:449–56

Stouffer PC, Bierregaard RO, Strong C, Lovejoy TE. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conserv. Biol.* 20:1212–23

Examines the effect of fragment size on hummingbird abundance over time.

Summerville KS, Crist TO. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 82:1360–70

Summerville KS, Crist TO. 2003. Determinants of lepidopteran community composition and species diversity in eastern deciduous forests: roles of season, eco-region and patch size. *Oikos* 100:134–48

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31:79–92

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, et al. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879–81

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, et al. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281–84

Tschapka M. 2004. Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. *J. Zool. Lond.* 263:7–21

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecol. Lett.* 8:857–74

Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* 89:944–51

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol. Appl.* 12:354–63

Tylianakis JM, Klein A-M, Tscharntke T. 2005. Spatiotemporal variation in the diversity of hymenoptera across a tropical habitat gradient. *Ecology* 86:3296–302

Vázquez DP, Morris WF, Jordano P. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecol. Lett.* 8:1088–94

Vu L. 2009. Diversity and similarity of butterfly communities in five different habitat types at Tam Dao National Park, Vietnam. *J. Zool.* 277:15–22

Weiblen GD. 2002. How to be a fig wasp. *Annu. Rev. Entomol.* 47:299–30

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG. 2010. Ecological and life history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143:2280–91

Williams NM, Kremen C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol. Appl.* 17:910–21

Williams PH, Osborne JL. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40:367–87

Willig MR, Presley SJ, Bloch CP, Hice CL, Yanoviak SP, et al. 2007. Phyllostomid bats of lowland Amazonia: effects of habitat alteration on abundance. *Biotropica* 39:737–46

Shows that some nectarivorous bats benefit from moderate levels of logging, whereas insectivorous feeding guilds respond negatively.

Winfree R. 2010. The conservation and restoration of wild bees. *Ann. NY Acad. Sci.* 1195:169–97

Winfree R, Aguilar R, Vazquez DP, LeBuhn G, Aizen M. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90:2068–76