Dispersal capacity and diet breadth modify the response of wild bees to habitat loss

Riccardo Bommarco, Jacobus C. Biesmeijer, Birgit Meyer, Simon G. Potts, Juha Pöyry, Stuart P. M. Roberts, Ingolf Steffan-Dewenter and Erik Öckinger

Supplementary data	"Data Supplement" http://rspb.royalsocietypublishing.org/content/suppl/2010/03/05/rspb.2009.2221.DC1.html
References	This article cites 48 articles, 7 of which can be accessed free http://rspb.royalsocietypublishing.org/content/277/1690/2075.full.html#ref-list-1
Subject collections	Articles on similar topics can be found in the following collections ecology (1764 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Proc. R. Soc. B* go to: **http://rspb.royalsocietypublishing.org/subscriptions**

Dispersal capacity and diet breadth modify the response of wild bees to habitat loss

Riccardo Bommarco[1],*, Jacobus C. Biesmeijer[2,3], Birgit Meyer[4], Simon G. Potts[5], Juha Pöyry[6], Stuart P. M. Roberts[5], Ingolf Steffan-Dewenter[4] and Erik Öckinger[1]

[1]*Department of Ecology, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden*
[2]*Institute of Integrative and Comparative Biology, and* [3]*Earth and Biosphere Institute, University of Leeds, Leeds LS2 9JT, UK*
[4]*Population Ecology Group, Department of Animal Ecology I, University of Bayreuth, 95440 Bayreuth, Germany*
[5]*Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, RG6 6AR, UK*
[6]*Finnish Environment Institute, Research Programme for Biodiversity, 00251 Helsinki, Finland*

Habitat loss poses a major threat to biodiversity, and species-specific extinction risks are inextricably linked to life-history characteristics. This relationship is still poorly documented for many functionally important taxa, and at larger continental scales. With data from five replicated field studies from three countries, we examined how species richness of wild bees varies with habitat patch size. We hypothesized that the form of this relationship is affected by body size, degree of host plant specialization and sociality. Across all species, we found a positive species–area slope ($z = 0.19$), and species traits modified this relationship. Large-bodied generalists had a lower z value than small generalists. Contrary to predictions, small specialists had similar or slightly lower z value compared with large specialists, and small generalists also tended to be more strongly affected by habitat loss as compared with small specialists. Social bees were negatively affected by habitat loss ($z = 0.11$) irrespective of body size. We conclude that habitat loss leads to clear shifts in the species composition of wild bee communities.

Keywords: habitat fragmentation; pollinator; body size; resource specialisation; sociality; *Bombus*

1. INTRODUCTION

Habitat loss and fragmentation pose a serious threat to biodiversity. Species inhabiting small remnant habitat fragments are expected to have high extinction rates owing to lower population sizes and increasing isolation from other conspecific populations (Hanski & Ovaskainen 2000; Fahrig 2003). In addition, the increasing relative amount of edge in small habitat patches may increase the abundance of habitat generalists and matrix species, which can negatively affect habitat specialists (Ewers & Didham 2006). The ability of a patch to support a certain number of species also depends on habitat quality (Thomas *et al*. 2001; Pöyry *et al*. 2009) that often deteriorates as a result of land use change and habitat loss (Kiviniemi & Eriksson 2002). All these mechanisms point to the critical importance of habitat patch size for understanding how communities respond to habitat loss.

In addition, it is important to take account of how species vary in their response to fragmentation. Extinction risk may be modified depending on species traits, i.e. shared ecological characteristics of the threatened species (Davies *et al*. 2000). Shifts in community composition from habitat loss may be masked when we only measure overall species richness, for instance, because of influx of generalist and matrix species into habitat fragments (Rand *et al*. 2006). This is poorly examined empirically for many ecologically important species groups providing key ecosystem functions such as pollination.

Dispersal capacity and niche breadth are two ecological characteristics that have been hypothesized as key determinants for the distribution of species abundances in fragmented landscapes (Ewers & Didham 2006) and for community organization in general (Blackburn & Gaston 2003). A common hypothesis is that species with a high dispersal capacity are better able to move between habitat patches, and they can more efficiently use a fragmented resource (Hanski & Ovaskainen 2000). According to this prediction, the typical positive relationship between species occurrence and habitat patch area in fragmented landscapes is expected to be more pronounced for poor compared with good dispersers (Roland & Taylor 1997; Öckinger & Smith 2006). Likewise, increased connectivity among patches in a landscape is expected to decrease the slope (z) of the relation between species number and habitat patch area (Connor & McCoy 1979; Drakare *et al*. 2006) and more so for poor compared with good dispersers (Lomolino 1984).

Another important ecological characteristic, niche breadth, is often measured by considering the degree of

* Author for correspondence (riccardo.bommarco@ekol.slu.se).

diet specialization. Species that can use multiple resources are expected to have a greater likelihood of fulfilling their resource requirements in a greater number of habitat patches (Roy et al. 1998; Swihart et al. 2003). Species with a restricted resource use are likely to meet these requirements only in a smaller subset of patches. As a result, species having a broad diet are expected to have a larger geographical range (Gaston 1988; Roy et al. 1998), and may be favoured in human-dominated landscapes (Johnson & Steiner 2000). In cases where a comprehensive analysis of species traits has been performed, information on dispersal ability and diet breadth has improved predictability of extinction risk (Kotiaho et al. 2005) and rarity (Hodgson 1993) for mobile invertebrates. Information is, however, lacking on how the incidence of species sharing these ecological characteristics is affected in landscapes where much of the focal habitat type has been lost. In addition, considering the recognized importance of both dispersal capacity and diet breadth, surprisingly few studies have explored the combined importance of these ecological characteristics on species distributions.

There is a broad lack of information on impacts by habitat loss and fragmentation on species in general, and of invertebrates in particular (Steffan-Dewenter & Tscharntke 2002) with a bias to butterflies as most often studied taxon (e.g. Steffan-Dewenter & Tscharntke 2000; Thomas & Hanski 2004). Considering the functional importance of bees as pollinators for wild and crop plants (Aguilar et al. 2006; Klein et al. 2007), surprisingly few studies have explored the direct effects of habitat loss on bee diversity (e.g. Krauss et al. 2009), and even fewer of these have considered species traits in this context. The studies that do consider shared traits for bees indicate that diet breadth can explain sensitivity to land use changes (Steffan-Dewenter et al. 2006; Moretti et al. 2009).

Sociality has also been shown to modify response to land use changes in bees, for instance as a result of contrasting habitat quality requirements for solitary as compared with stingless social bees in the tropics (Aizen & Feinsinger 1994; Klein et al. 2003). In temperate areas, where social bees are represented both by large-bodied bumble-bees and also by some smaller bodied Halictid bees in the genera *Halictus* and *Lasioglossum*, it is largely unknown if sociality can buffer impacts of habitat fragmentation. A possibility is, for instance, that social bees are better able to access resources in intensively managed agricultural landscapes with few remaining semi-natural habitats (Steffan-Dewenter et al. 2002) and that at least some species can also exploit mass flowering crops in the landscape surrounding nesting habitats (Westphal et al. 2003).

In this study, we examine the relationship between wild bee species richness and reductions in habitat size of patches of semi-natural grasslands in Northern and Central Europe. By coupling data on species occurrence in grassland patches from five separate studies in Finland, Germany and Sweden, with information on bee species traits, we were able to examine the general response of a functionally important group of species to habitat loss. We assessed whether body size, which is closely correlated to mobility in bees (Greenleaf et al. 2007), and degree of diet specialization modifies the response of bees to habitat

loss. We also considered possible effects of level of sociality in combination with these traits. Our predictions were that (i) overall species richness will increase with patch area; (ii) small-bodied species with limited dispersal capacity and with narrow feeding niches will be particularly sensitive to habitat loss and will therefore demonstrate a strong positive relationship between species richness and habitat patch area; and (iii) sociality will buffer the effects of habitat loss as a result of the enhanced foraging and reproductive capacity of social bees.

2. MATERIAL AND METHODS

(a) *Sampling of bees*
We used data from five studies published previously or in preparation for publication from three European countries; Finland, Germany and Sweden (table 1). All studies focused on discrete habitat patches surrounded by a matrix dominated by human land use (mainly agriculture and commercial forestry). The habitat patches consisted of different types of semi-natural grasslands or limestone quarries (table 1). In all studies, bees were sampled by similar and standardized transect counts during one season, but with slightly different sampling efforts. Details on sampling methods from each of the five studies are given below.

(b) *Limestone quarries in Germany*
The transect covered all vegetation types in the quarries. Each quarry was visited seven times between 19 April and 3 September 1999. The sampling effort was adjusted to habitat area. Transect time in small quarries <0.1 ha was 15 min, in sites $0.1-0.5$ ha it was 30 min, in sites $0.5-1.0$ ha it was 45 min, in sites $1.0-3.0$ ha it was 60 min, in sites $3.0-10.0$ ha it was 75 min and in quarries larger than 10.0 ha it was 90 min. The width of the strip transect in which the observer searched for bees was 2 m (Krauss et al. 2009).

(c) *Calcareous grassland in Germany*
Each grassland patch was visited six times from April to September 2004. Bees were recorded within a 4 m wide strip transect on sunny days with little wind. The sampling effort was adjusted to habitat area. Transect time varied from 20 min in 11 small fragments ($314-1133$ m^2), to 40 min in 13 medium fragments ($0.1-0.8$ ha), and 60 min in eight large fragments ($1.1-5.1$ ha).

(d) *Dry grassland in Finland*
Within each grassland patch, a 0.07 ha sampling square of dry grassland delimited within a larger grassland area (which typically consisted of a mosaic of dry and mesic grassland types) was established. Bees were sampled along a serpentine-shaped transect with a length of 150 m and a width of 5 m. Each site was visited four times between early June and early August in the summer of 2004.

(e) *Mesic grassland in Finland*
Bees were sampled using the transect method as above but along a transect with a length of 350 m and width of 5 m within a 0.25 ha sampling square placed in the focal grassland. The grassland area outside the 0.25 ha sampling square was searched for a time period that was logarithmically related to the remaining area (Pöyry et al. 2009). Each site was visited four times between early May and late August during the summer of 2001.

Table 1. Description of the five datasets included in the study. The geographical coordinates indicate the approximate centre point of each study area.

country	geographical coordinates	habitat type	number of species	number of patches	patch area (min–max) (ha)	patch distances (median, max–min) (km)	number of resamplings	reference
Finland	60°12′ N, 25°12′ E	dry semi-natural grasslands	82	40	0.07–6.5	4.0 (0.2–42.4)	4	J. Pöyry, J. Paukkunen & M. Kuussaari 2004, unpublished data
Finland	61°00′ N, 25°00′ E	mesic semi-natural grasslands	68	48	0.25–6.0	12.0 (3.7–29.7)	4	J. Pöyry, J. Paukkunen & M. Kuussaari 2001, unpublished data
Germany	51°32′ N, 9°55′ E	limestone quarries	76	24	0.01–21.2	n.a.	7	Krauss *et al.* (2009)
Germany	51°32′ N, 9°55′ E	calcareous grasslands	79	32	0.03–5.1	14.6 (0.3–30.6)	6	B. Meyer, J. Krauss & I. Steffen-Dewenter 2004, unpublished data
Sweden	58°58′ N, 16°40′ E	semi-natural pastures	65	45	1.9–16.3	56.9 (3.5–294)	4	R. Bommarco & E. Öckinger 2007, unpublished data

(f) *Semi-natural pastures in Sweden*

Each site was visited four times from 27 May to 1 August 2007. Sampling effort was adjusted to patch area by setting the length of transects proportional to patch area with $50 \, m \, ha^{-1}$ (and rounded off to the nearest 50 m). The width of the sampling strip transect was 2 m.

(g) *Patch area and connectivity*

Patch areas were measured from aerial photos or digitized maps and ranged from 0.009 to 21.2 ha (table 1). Measures of connectivity among patches were not available for the limestone quarry dataset. In addition, connectivity measures were derived differently among datasets, and therefore we chose not to consider connectivity as a predictor in the current study.

(h) *Ecological characteristics of bee species*

Each bee species was described using three species traits that are known to be important for bee ecology (e.g. Westrich 1990; Michener 2000). Firstly, diet breadth was assigned as oligolectic (specialist) for bees that collect pollen only from plants within the same plant family, or polylectic (generalist) for bees that collect pollen from different plant families based on information from the literature and expert observations. Cleptoparasitic species (cuckoo bees) were excluded from this part of the analyses as they do not collect pollen.

Secondly, bee body size was measured as the inter-tegular distance (ITD), which is the distance (millimetre) between the two insertion points, tegulae, of the wings. This measure is strongly correlated with species mobility (Greenleaf *et al.* 2007). Only female specimens were measured. For social bees, the ITD of queens and not workers was measured. Colony fitness is highly dependent upon the interaction of the queens with the landscape as they are responsible for the nest establishment and early development of the whole colony (Heinrich 1979). The median ITD for all species,

2.23 mm, was used as a cut-off value to assign species as large (ITD > 2.23 mm) or small (ITD < 2.23 mm). Body size categories were used because it is difficult to perform analysis on continuous body sizes when using species richness as dependent variable. The effects of presence–absence using continuous body size would entail estimation of binomial distribution for each species individually which is problematic for the many species that occur at low rates.

Finally, all species were categorized into two classes according to degree of sociality following Michener (2000). Subsocial (bumble-bees) and primitively eusocial species (some Halictidae) were pooled as social, and all other species were categorized as solitary. Four species for which degree of sociality is unknown were removed from analyses that involved sociality. As *Apis mellifera* (honey bees) are domesticated in the study areas and are subject to human movements of colonies, all *A. mellifera* observations were excluded prior to the analyses (see appendix in the electronic supplementary material). The nomenclature of the bees follows Michener (2000).

(i) *Statistical analysis*

Species richness was log-transformed $(\log_{10}(n + 1))$ and used as dependent variable in mixed effect models. We built random-effect models where slopes and intercepts for each trait combination were allowed to vary among datasets. Such model assumptions allow for construction of highly general and predictive models as the studied samples are considered a subset of a larger target population (Littell *et al.* 2006). The variation in sampling effort among studies is considered by including dataset as random factor, and is expected to increase variability in the estimation of slopes among studies. As we had a balanced design with all trait categories measured in each patch but with varying number of patches among studies, we used the Satterthwaite method to calculate the degrees of freedom (Littell *et al.* 2006).

We first analysed overall effects of $\log_{10}$ habitat area on $\log_{10}$ bee species richness irrespective of body size or dispersal capacity of the species, with study and slope $\times$ study assigned as random factors, in order to obtain an estimate of the z-value of the species–area curve.

We then analysed $\log_{10}$ bee species richness using analyses of covariance that included both habitat area and trait categories in the model to probe whether z-slopes were affected by traits. Firstly, we analysed a model including $\log_{10}$ habitat area, classes of body size and degree of specialization, and all possible interactions between habitat area and trait classes. A significant interaction between area and one of the trait factors would imply that the relationship between species richness and habitat area differs between the trait classes. A second analysis focused on effects of sociality that had to be considered separately as there were no social diet specialists in the data. Here, we included classes of body size and sociality together with all possible interactions between habitat area and the trait classes. We performed post hoc analyses in which we regressed $\log_{10}$ bee species richness against $\log_{10}$ habitat area for each combination of body size and specialization classes, and of body size and sociality in order to estimate z-values. We used pairwise post hoc tests to find between which of the trait classes differences in z-values were statistically significant. In all analyses that included trait classes, the following parameters were assigned as random factors: study, site nested within study, study $\times$ body size $\times$ diet specialization (or sociality) and slope $\times$ study $\times$ body size $\times$ diet specialization (or sociality). This random structure was also used for estimation of species–area slopes. We used Proc Mixed in SAS 9.1 for Linux for all statistical analyses (SAS 2009).

3. RESULTS

A total of 138 species were included in the analysis. Of these, 23 were large-bodied and 14 small-bodied diet specialists (oligolectic) species, and 42 were large-bodied and 59 small-bodied diet generalists (polylectic) species. There was a taxonomic spread among groups of diet specialization and body size groups. The subfamilies Andreninae, Colletinae and Megachilinae were represented by species in all four trait groups. Apinae was represented in three groups, Halictinae in two and all four species of Melittinae fell within the group of oligolectic bees with large bodies (appendix in the electronic supplementary material).

All social bees were categorized as diet generalists. Of the social bees, 10 were small- and 15 were large-bodied. Information on sociality was missing for four small-bodied diet generalist species. The group with social and large bees contained only and every *Bombus* species (i.e. bumble-bees). The social and small-bodied group contained species from the genera *Halictus* and *Lasioglossum*. Differences between large- and small-bodied social bees could therefore not be separated from potential differences owing to phylogeny. The bee species sampled in the entire study are listed in the appendix in the electronic supplementary material, together with information on the study in which a species was observed, ITD value, degree of diet specialization and sociality.

The total species richness of wild bees in a given patch was to a large extent explained by habitat patch size. The relationship between $\log_{10}$ species richness and $\log_{10}$

Table 2. Results from mixed effects model for effects of log habitat area on $\log_{10}$ species richness of species groups sharing trait characteristics. We found significant three-way interactions between trait variables and habitat area. The first analysis examines effects of habitat patch area in relation to species richness for diet specialists, diet generalists, large- and small-bodied bee species. The second analysis, which included diet generalists only, estimated effects of habitat patch size on species richness depending on sociality and body size. A significant interaction between log area and trait categories indicates that there is a difference between species–area slope for species belonging to different trait groups.

analysis	effect	d.f.	F	p
(1) diet breadth and body size				
	log area	1,17.6	34.6	<0.0001
	specialization	1,11.2	127.9	<0.0001
	body size	1,11.2	0.03	0.86
	specialization × body size	1,11.2	0.08	0.78
	log area × specialization	1,9.3	1.1	0.32
	log area × body size	1,9.3	0.45	0.52
	log area × body size × specialization	1,9.3	5.7	0.04
(2) sociality and body size				
	log area	1,17.8	24.1	0.0001
	sociality	1,12	0.39	0.55
	body size	1,12	0.20	0.66
	sociality × body size	1,12	20.0	0.0008
	log area × sociality	1,12	0.82	0.38
	log area × body size	1,12	2.9	0.11
	log area × sociality × body size	1,12	0.25	0.63

habitat area across all studies and bee species was estimated to be $z = 0.19$ (s.e. $= 0.041$, $F_{1,3} = 4.72$, $p = 0.02$). The slope of this relationship, however, depended on species-specific trait characteristics. In the first traits analysis, we found a significant three-way interaction of $\log_{10}$ habitat area, diet breadth and body size on $\log_{10}$ species richness (table 2).

The three-way interaction was analysed in post hoc analyses and the relationship between $\log_{10}$ species richness and $\log_{10}$ habitat area (z-values) was estimated for each trait combination (figure 1). Using a pairwise post hoc test, we found that diet generalists with poor dispersal capacity, i.e. small-bodied diet generalist bees, had higher z compared with large-bodied generalists ($p = 0.04$), and marginally significantly higher z than diet-specialized (oligolectic) bees with small bodies ($p = 0.06$) (figure 1). Other pairwise comparisons between trait groups did not give significant differences ($p > 0.25$). Slopes for all trait categories were significantly larger than zero. Large-bodied resource generalists performed better in landscapes highly impacted by habitat loss as their z-value was closest to zero ($p = 0.06$) (figure 1).

In a second analysis where we only considered generalist (i.e. polylectic) species, we found no significant three-way interaction of $\log_{10}$ habitat area, sociality and body size on $\log_{10}$ species richness (table 2). Model reductions rendered no significant differences in z among trait groups. The estimated z-value for social bees was 0.11 and differed significantly from zero slope (s.e. $= 0.03$, d.f. $= 9.15$, $t = 3.8$, $p = 0.004$).
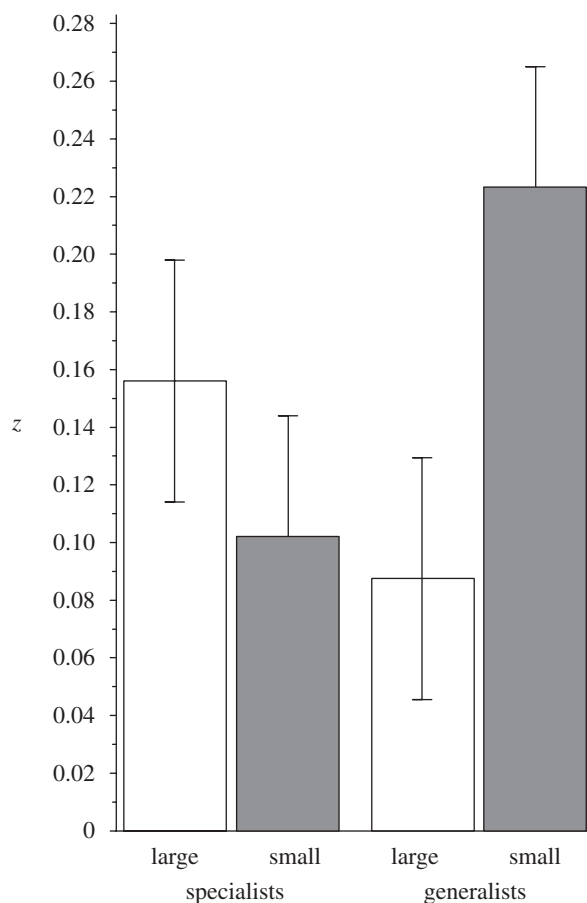
Figure 1. Model estimates of slopes and standard errors of species−area curves (z). The slope z indicates differences in rate of change in species richness with patch area among large- and small-bodied bee species that are either diet specialists or generalists. Pairwise post hoc test gave significant differences only between small- and large-bodied diet generalists, and near significance between small-bodied generalist and small-bodied specialist bees ($p = 0.06$).

4. DISCUSSION

The quantitative synthesis of the effects of habitat loss on wild bees demonstrates, in accordance with our prediction, that wild bee species richness increases with habitat patch size. The estimated slope (z) of the species−area curve was 0.19, which is a relatively high value for mainland populations in habitat fragments. It is comparable with the slope found for species (mainly vertebrates and plants) on true islands (Rosenzweig 1995), and is much higher than for other flower visiting invertebrates such as butterflies (Steffan-Dewenter & Tscharntke 2000; Krauss *et al.* 2003; Öckinger *et al.* 2009).

Importantly, life-history traits associated with diet niche breadth and dispersal capacity modified the response of wild bee species to habitat loss. This indicates that not only species richness, but also species composition changes with increasing habitat loss (McKinney & Lockwood 1999). Other than harbouring fewer bee species, small remaining habitat patches tend to lose small and specialized species while retaining mainly the large-bodied diet generalists. Because bees are part of mutualistic interaction networks with plants that require insect pollination for their reproduction, changes in bee species composition may lead to changes in plant assemblages and their

associated fauna and could have potentially severe implications for the functioning of the whole ecosystem (Biesmeijer *et al.* 2006; Fortuna & Bascompte 2006).

In accordance with our predictions, the small-bodied generalist species were more impacted by habitat loss (i.e. they had a steeper slope of the species−area relationship) than large-bodied generalists. Furthermore, species with a broad dietary niche seemed less impacted by habitat loss than were diet specialists, at least so for large species (figure 1), but this difference was not statistically significant. The results confirm general predictions from ecological theory and previous findings for other invertebrate taxa in fragmented landscapes (Steffan-Dewenter & Tscharntke 2002). The vague support in previous studies for shifts in body size and diet breadth distributions in communities affected by habitat loss (e.g. Henle *et al.* 2004) may be explained by the fact that combinations of these traits have not generally been considered. There is also a risk in the current study of falsely rejecting the possibility of true differences (type II error) owing to variable sampling efforts, and low replication and therefore statistical power. Reliable ecological information of diet breadth is largely lacking and should be based on repeated observations of diet preference for multiple individuals of each species from locations with shared resources (Kleijn & Raemakers 2008). Our analysis, which is based on, for bees unique, but comparatively coarse available information, clearly suggests that more detailed information on the interplay between diet selection and resource availability is needed to better understand the effects of land use change on biodiversity.

Contrary to our prediction, small-bodied diet specialists tended to be less impacted by habitat loss as compared with large-bodied specialists. A possible explanation is that a high proportion of the small specialist bees have already become extinct even from the large habitat patches, which is supported by the fact that overall species richness of diet specialists was comparably low. In addition, we found that the species richness of large-bodied species with a narrow dietary niche tended to decrease at the same or somewhat faster rate with decreasing habitat patch size compared with bees with small bodies. The sensitivity to habitat loss has been found to increase with body size in other taxa (Crooks 2002; Ewers & Didham 2006), and this may have several explanations. For instance, large-bodied organisms are expected to have smaller population sizes, and they may be more sensitive to predation, thereby having a greater risk of extinction. The prediction that small-bodied species should be more sensitive to habitat loss is based on the observation that body size (ITD) generally correlates with bee mobility (Greenleaf *et al.* 2007), and species with low mobility are predicted to be particularly sensitive to habitat loss. However, butterfly species with moderate dispersal ability have been found to exhibit the highest sensitivity to the effects of habitat loss (Thomas 2000). This may be because species with very low dispersal rates will also show the lowest mortality linked to dispersal in highly fragmented landscapes, compared with species with better dispersal capacity. In addition, a large body also implies larger energetic needs and such species may also depend upon resources from multiple patches. Indeed, body size may also be correlated with other life-history traits that are associated

with the degree of specialization for which we have currently no information, but which could potentially influence extinction risk. It is clear that more studies are needed on how dispersal ability, but also dispersal mechanism, modifies species responses in changing landscapes (Montoya *et al.* 2008).

When considering the effects of sociality (which was only relevant for polylectic bees), no overall effect could be detected on the species–area curves. We found that large-bodied social bees (this group consisted entirely of *Bombus* spp.) were affected similarly by habitat loss as small-bodied social bees (*Lasioglossum* spp. and *Halictus* spp.). Because of this strict taxonomic division into the body size groups, we could not separate possible effects of body size from intrinsic phylogenetic differences. However, it seems that there is some common feature among social bees that make them similarly sensitive to habitat loss, regardless of body size or taxonomy. A relatively high foraging and reproductive capacity in social bees may buffer negative effects of diminishing availability for food resources in fragmented landscapes. Building colonies requires a relatively long season and carries relatively large resource requirements. Social bees therefore often have extended foraging seasons and are able to use a wide range of resources (Michener 2000). In addition, at least *Bombus* sp. have a high size diversity among their workers, which is not captured in a single ITD measurement, which allows them to exploit a wider range of floral resources. However, nest site availability could become a limiting resource when habitat is lost irrespective of body size, and this can explain the positive species–area relationship for social species.

Effects of land use change on social versus solitary species differ between studies from different biogeographical regions. Social stingless bees have been found to be more sensitive to land use change in studies from the tropics (e.g. Aizen & Feinsinger 1994; Klein *et al.* 2003). Previous studies from temperate areas have found that the social bumble-bees are less sensitive than solitary bees (Steffan-Dewenter *et al.* 2002). However, recent studies have revealed that bumble-bee communities are sensitive to habitat isolation and resource separation in the landscape (Öckinger & Smith 2007; Rundlöf *et al.* 2008). Our results confirm this as bumble-bee species richness decreased with reduced habitat size ($z = 0.11$).

In a recent meta-analysis, habitat loss was found to be a key anthropogenic disturbance causing bee declines (Winfree *et al.* 2009). Exploring species–area effects in semi-natural habitats, which are identified as high value habitats for bee diversity, is a first step to explore links between land use and loss of bee species. It is, however, an oversimplification to regard such remnant habitats as analogous to oceanic islands surrounded by a hostile matrix (Brotons *et al.* 2003; Prugh *et al.* 2008). The land use and disturbance regime in the human-dominated landscape surrounding the focal habitat patches in the current study will probably modify species–area responses for bees. Maintaining and restoring a variety of habitat types that provide nest sites and pollen resources within foraging range (Franzén & Nilsson 2010), increasing habitat connectivity and softening the matrix (Donald & Evans 2006) are likely to affect bee species richness positively. Such landscape effects

remain to be systematically explored for bees, but are likely to be most effective in intensively used landscapes where much key habitat has been lost (Holzschuh *et al.* 2007; Rundlöf *et al.* 2008).

Basic information on the life history and ecology is lacking for many major taxa that are under pressure from habitat loss and other human-induced environmental changes. In the current study, variability in species–area relationships for wild bees could be explained by including information on shared ecological traits. By including primary data from multiple studies, we can make general predictions about species distributions in changing landscapes. The results indicate that traits linked to important ecological processes such as dispersal, resource utilization and reproduction warrant consideration in this context. By including traits, we obtained information on significant shifts in species composition owing to land use conversion with potential implications for conservation of biodiversity, ecosystem functions and provisioning of services.

REFERENCES

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M. A. 2006 Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* **9**, 968–980. (doi:10.1111/j.1461-0248.2006.00927.x)

Aizen, M. A. & Feinsinger, P. 1994 Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine chaco serrano. *Ecol. Appl.* **4**, 378–392. (doi:10.2307/1941941)

Biesmeijer, J. C. *et al.* 2006 Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science* **313**, 351–354. (doi:10.1126/science.1127863)

Blackburn, T. M. & Gaston, K. J. 2003 *Macroecology: concepts and consequences.* Oxford, UK: Blackwell science.

Brotons, L., Mönkkönen, M. & Martin, J. L. 2003 Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *Am. Nat.* **162**, 343–357. (doi:10.1086/376887)

Connor, E. F. & McCoy, E. D. 1979 Statistics and biology of the species–area relationship. *Am. Nat.* **113**, 791–833. (doi:10.1086/283438)

Crooks, K. R. 2002 Relative sensitivities of mammalian carnivores to habitat fragmentation. *Cons. Biol.* **16**, 488–502. (doi:10.1046/j.1523-1739.2002.00386.x)

Davies, K. F., Margules, C. R. & Lawrence, K. F. 2000 Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450–1461. (doi:10.1890/0012-9658(2000)081[1450:WTOSPP]2.0.CO;2)

Donald, P. F. & Evans, A. D. 2006 Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *J. Appl. Ecol.* **43**, 209–218. (doi:10.1111/j.1365-2664.2006.01146.x)

Drakare, S., Lennon, J. J. & Hillebrand, H. 2006 The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecol. Lett.* **9**, 215–227. (doi:10.1111/j.1461-0248.2005.00848.x)

Ewers, R. M. & Didham, R. K. 2006 Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* **81**, 117–142. (doi:10.1017/S1464793105006949)

Fahrig, L. 2003 Effects of habitat fragmentation on biodiversity. *Ann. Rev. Ecol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)

Fortuna, M. A. & Bascompte, J. 2006 Habitat loss and the structure of plant–animal mutualistic networks. *Ecol. Lett.* **9**, 278–283. (doi:10.1111/j.1461-0248.2005.00868.x)

Franzén, M. & Nilsson, S. G. 2010 Both population size and patch quality affect local extinctions and colonizations. *Proc. R. Soc. B* **277**, 78–85. (doi:10.1098/rspb.2009.1584)

Gaston, K. J. 1988 Patterns in local and regional dynamics of moth populations. *Oikos* **53**, 49–57. (doi:10.2307/3565662)

Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. 2007 Bee foraging ranges and their relationship to body size. *Oecologia* **153**, 589–596. (doi:10.1007/s00442-007-0752-9)

Hanski, I. & Ovaskainen, O. 2000 The metapopulation capacity of a fragmented landscape. *Nature* **404**, 755–758. (doi:10.1038/35008063)

Heinrich, B. 1979 *Bumblebee economics*. Cambridge, MA: Harvard University Press.

Henle, K., Davies, K. F., Kleyer, M., Margules, C. & Settele, J. 2004 Predictors of species sensitivity to fragmentation. *Biodiv. Cons.* **13**, 207–251. (doi:10.1023/B:BIOC.0000004319.91643.9e)

Hodgson, J. G. 1993 Commonness and rarity in British butterflies. *J. Appl. Ecol.* **30**, 407–427. (doi:10.2307/2404182)

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, 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. (doi:10.1111/j.1365-2664.2006.01259.x)

Johnson, S. D. & Steiner, K. E. 2000 Generalization versus specialization in plant pollination systems. *TREE* **15**, 140–143. (doi:10.1016/S0169-5347(99)01811-X)

Kiviniemi, K. & Eriksson, O. 2002 Size-related deterioration of semi-natural grassland fragments in Sweden. *Div. Dist.* **8**, 21–29. (doi:10.1046/j.1366-9516.2001.00125.x)

Kleijn, D. & Raemakers, I. 2008 A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* **89**, 1811–1823. (doi:10.1890/07-1275.1)

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. 2003 Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.* **40**, 837–845. (doi:10.1046/j.1365-2664.2003.00847.x)

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B.* **274**, 303–313. (doi:10.1098/rspb.2006.3721)

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. (doi:10.1073/pnas.0406718102)

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. 2003 How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *J. Biogeogr.* **30**, 889–900. (doi:10.1046/j.1365-2699.2003.00878.x)

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. (doi:10.1111/j.1365-2664.2008.01582.x)

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D. & Schabenberger, O. 2006 *SAS for mixed models*, 2nd edn. Cary, NC: SAS Institute Inc.

Lomolino, M. V. 1984 Mammalian island biogeography: effects of area, isolation and vagility. *Oecologia* **61**, 376–382. (doi:10.1007/BF00379638)

McKinney, M. L. & Lockwood, J. L. 1999 Biotic homogenization: a few winners replacing many losers in the next mass extinction. *TREE* **14**, 450–453. (doi:10.1016/S0169-5347(99)01679-1)

Michener, Ch. D. 2000 *The bees of the world*. Baltimore, MD: Johns Hopkins University Press.

Montoya, D., Zavala, M. A., Rodriguez, M. A. & Purves, D. W. 2008 Animal versus wind dispersal and the robustness of tree species to deforestation. *Science* **320**, 1502–1504. (doi:10.1126/science.1158404)

Moretti, M., de Bello, F., Roberts, S. P. M. & Potts, S. G. 2009 Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *J. Anim. Ecol.* **78**, 98–108. (doi:10.1111/j.1365-2656.2008.01462.x)

Öckinger, E. & Smith, H. G. 2006 Landscape composition and habitat area affect butterfly species richness. *Oecologia* **149**, 526–534. (doi:10.1007/s00442-006-0464-6)

Öckinger, E. & Smith, H. G. 2007 Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol.* **44**, 50–59. (doi:10.1111/j.1365-2664.2006.01250.x)

Öckinger, E., Franzén, M., Rundlöf, M. & Smith, H. G. 2009 Mobility-dependent effects on species richness in fragmented landscapes. *Basic Appl. Ecol.* **10**, 573–578. (doi:10.1016/j.baae.2008.12.002)

Pöyry, J., Paukkunen, J., Heliölä, J. & Kuussaari, M. 2009 Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. *Oecologia* **160**, 577–587. (doi:10.1007/s00442-009-1328-7)

Prugh, L. R., Hodges, K. E., Sinclair, A. R. E. & Brashares, J. S. 2008 Effect of habitat area and isolation on fragmented animal populations. *Proc. Natl Acad. Sci. USA* **105**, 20 770–20 775. (doi:10.1073/pnas.0806080105)

Rand, T. A., Tylianakis, J. M. & Tscharntke, T. 2006 Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* **9**, 603–614. (doi:10.1111/j.1461-0248.2006.00911.x)

Roland, J. & Taylor, P. D. 1997 Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**, 710–713. (doi:10.1038/386710a0)

Rosenzweig, M. L. 1995 *Species diversity in space and time*. Cambridge, MA: Cambridge University Press.

Roy, D. B., Quinn, R. M. & Gaston, K. J. 1998 Coincidence in the distribution of butterflies and their food plants. *Ecography* **21**, 279–289. (doi:10.1111/j.1600-0587.1998.tb00565.x)

Rundlöf, M., Nilsson, H. & Smith, H. G. 2008 Interacting effects of farming practice and landscape context on bumble-bees. *Biol. Cons.* **141**, 417–426.

SAS. 2009 *SAS Institute*. Cary, NC, USA.

Steffan-Dewenter, I. & Tscharntke, T. 2000 Butterfly community structure in fragmented habitats. *Ecol. Lett.* **3**, 449–456. (doi:10.1111/j.1461-0248.2000.00175.x)

Steffan-Dewenter, I. & Tscharntke, T. 2002 Insect communities and biotic interaction on fragmented calcareous

grasslands—a mini review. *Biol. Cons.* **104**, 275–284. (doi:10.1016/S0006-3207(01)00192-6)

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. 2002 Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421–1432. (doi:10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2)

Steffan-Dewenter, I., Klein, A. M., Gaebele, V., Alfert, T. & Tscharntke, T. 2006 Bee diversity and plant–pollinator interactions in fragmented landscapes. In *Plant–pollinator interactions: from specialization to generalization* (eds N. M. Waser & J. Ollerton), pp. 387–407. Chicago, IL, USA: University of Chicago Press.

Swihart, R. K., Gehring, T. M., Kolozsvary, M. B. & Nupp, T. E. 2003 Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Div. Dist.* **9**, 1–18. (doi:10.1046/j.1472-4642.2003.00158.x)

Thomas, C. D. 2000 Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. Lond. B.* **267**, 139–145. (doi:10.1098/rspb.2000.0978)

Thomas, C. D. & Hanski, I. 2004 Metapopulation dynamics in changing environments: butterfly responses to habitat and climate change. In *Ecology, genetics and evolution of metapopulations.* (eds I. Hanski & O. E. Gaggiotti), pp. 489–514. Amsterdam, The Netherlands: Elsevier Academic Press.

Thomas, J. A., Bourn, N. A. D., Clarke, R. T., Stewart, K. E., Simcox, D. J., Pearman, G. S., Curtis, R. & Goodger, B. 2001 The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc. R. Soc. Lond. B.* **268**, 1791–1796. (doi:10.1098/rspb.2001.1693)

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. 2003 Mass flowering crops enhance pollinator densities at a landscape scale. *Ecol. Lett.* **6**, 961–965. (doi:10.1046/j.1461-0248.2003.00523.x)

Westrich, P. 1990 *Die Wildbienen Baden-Württembergs. Allgemeiner Teil.* Stuttgart, Germany: Ulmer Verlag.

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G. & Aizen, M. A. 2009 A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**, 2068–2076. (doi:10.1890/08-1245.1)