



Ecological and life-history traits predict bee species responses to environmental disturbances

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ARTICLE INFO

Article history:

Received 11 August 2009

Received in revised form 9 March 2010

Accepted 21 March 2010

Available online 24 April 2010

Keywords:

Anthropogenic disturbance

Bees

Functional traits

Landscape change

Life-history response guilds

ABSTRACT

The ability to predict the responses of ecological communities and individual species to human-induced environmental change remains a key issue for ecologists and conservation managers alike. Responses are often variable among species within groups making general predictions difficult. One option is to include ecological trait information that might help to disentangle patterns of response and also provide greater understanding of how particular traits link whole clades to their environment. Although this “trait-guild” approach has been used for single disturbances, the importance of particular traits on general responses to multiple disturbances has not been explored. We used a mixed model analysis of 19 data sets from throughout the world to test the effect of ecological and life-history traits on the responses of bee species to different types of anthropogenic environmental change. These changes included habitat loss, fragmentation, agricultural intensification, pesticides and fire. Individual traits significantly affected bee species responses to different disturbances and several traits were broadly predictive among multiple disturbances. The location of nests – above vs. below ground – significantly affected response to habitat loss, agricultural intensification, tillage regime (within agriculture) and fire. Species that nested above ground were on average more negatively affected by isolation from natural habitat and intensive agricultural land use than were species nesting below ground. In contrast below-ground-nesting species were more negatively affected by tilling than were above-ground nesters. The response of different nesting guilds to fire depended on the time since the burn. Social bee species were more strongly affected by isolation from natural habitat and pesticides than were solitary bee species. Surprisingly, body size did not consistently affect species responses, despite its importance in determining many aspects of individuals’ interaction with their environment. Although synergistic interactions among traits remain to be explored, individual traits can be useful in predicting and understanding responses of related species to global change.

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1. Introduction

Ecologists and environmental scientists often need to monitor and predict how communities might respond to environmental disturbance, change over landscape gradients or vary among different habitats. However, this task is fraught with uncertainty for many reasons. For many taxa, we know little about critical population dynamic variables, physiological tolerances, ecological constraints, or long-term and indirect effects (Davidson et al., 1984; Roemer, 2002). One useful approach toward removing uncertainty in how species respond would be to incorporate widely-available

information about their biology and look for consistent responses within groups that share traits (Henle et al., 2004). Such an approach would help ecologists to predict general patterns that could be applied to a range of related taxa and provide a mechanistic link between disturbances and patterns of response within communities. As such, it would also be of clear conservation value when land managers and stakeholders face decisions associated with landscape or global changes and how these might impact communities or particular species of conservation concern.

In recent years, ecologists have identified key population, life-history and ecological attributes that influence how species respond to landscape changes such as habitat loss and fragmentation. Population demographic variables (e.g., intrinsic growth rate, variation in population size) are expected to directly

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determine changes in abundance and mediate extinction risk (e.g., Pimm et al., 1993; Settele and Poethke, 1996; Fagan et al., 1999). Although population dynamic traits provide species-level mechanisms for why species may decline, many such traits are difficult to measure and their relation to population decline or extinction appears to be variable. For example, population stability and dispersal negatively correlate with extinction risk for some species but show no relation or even positive relation in others (reviewed in Henle et al. (2004)). The use of ecological variables offers a valuable alternative to assessing demographic variables that has been explored mostly in the context of habitat loss and fragmentation (McKinney, 1997; Davies et al., 2000; Zayed et al., 2004; Kolb and Diekmann, 2005; Cane et al., 2006; Devictor et al., 2008). Ecological and behavioral traits are usually consistent among populations of a species, are often easier to assess than population demographic variables, and are associated with various environmental variables of interest. For example, traits, such as body size, that determine the spatial scale at which the organisms perceive their environment and govern access to resources of various kinds (mineral nutrients, prey items, nest sites, pollinators, e.g., Lavorel and Garnier, 2002; Stoks and McPeck, 2003; Larsen et al., 2005; Petchey and Gaston, 2006) affect species turnover among habitats, along environmental gradients or between regions (Mason et al., 2007). These same sorts of traits are likely to determine the sensitivity of species to anthropogenic disturbance (Lavorel and Garnier, 2002; Goulson et al., 2005; Larsen et al., 2005; Rundlöf et al., 2008; Jauker et al., 2009; Moretti et al., 2009).

Identifying common life-history or ecological traits that affect the sensitivity of species to environmental change may allow for greater insight into community responses beyond simple changes in species richness. If such traits commonly determine species responses to disturbance, then we should expect not only species loss following disturbance, but specific shifts in community or guild composition. Furthermore, if the traits that determine species response to environmental change or disturbance positively correlate with those that determine functional importance, then functional trait composition and overall ecosystem function may also change dramatically (Lavorel and Garnier, 2002; Larsen et al., 2005; Petchey and Gaston, 2006).

In this paper, we examine how species in one monophyletic group of ecologically and economically important organisms, the bees, respond to different types of disturbance using data from 19 studies worldwide. Pollinators, including bees, are a keystone group thought to be threatened by human disturbance (Biesmeijer et al., 2006; NRC-USA, 2007). Between 62% and 75% of flowering plants rely on animal pollinators for sexual reproduction (Burd, 1994; Ashman et al., 2004), an estimated 76% of crop species used by humans benefit in production from animal pollination, (mostly by insects) (Klein et al., 2007), and globally pollination services are estimated to be worth €153 billion a year (Gallai et al., 2009). We use bees not only because of their functional importance, but also because they vary in multiple ecological and life-history traits.

Like other taxa, bees' sensitivity to environmental change, including anthropogenic disturbance, is likely to depend on traits that determine species mobility, access to and requirements for nesting and forage resources, or physiological tolerance. We selected a set of such life-history and ecological traits that are thus likely to affect responses to habitat change and that could be assigned reliably from the literature, or measured directly among diverse taxa. Traits included body size, nest location, method of nest construction, sociality and trophic specialization. We then tested whether these traits significantly affected the response of species to five common environmental disturbances. We predicted that the analyses including specific traits might reveal general response patterns that depend on life-history or ecological characteristics of bee species. Such patterns would not always be visible when the

entire bee community was compared before and after the disturbance.

We selected disturbances recognized as among those strongly affecting animal populations and biodiversity globally including habitat loss, agricultural intensification (Green et al., 2005; Fischer and Lindenmayer, 2007; Kleijn et al., 2009) and grazing. We also chose several disturbances likely to affect bees because of their ecology and association with flowers and cultivated plant populations. These included fire, tilling and pesticide use (Gels et al., 2002; Shuler et al., 2005).

Our analysis differs importantly from some recent studies that have explored the role of functional traits in how species respond to disturbance in that we use individual species as replicates in mixed model analyses. Past studies have either pooled abundance across multiple species that share a common trait, or examined changes in species richness for groups with a specified trait (Moretti et al., 2009; Winfree et al., 2009; Williams unpublished). However, pooling species with the same life-history traits might mask general responses. For example, if most trophic specialists decreased in response to fire but one abundant species increased, numbers of the abundant species could obscure declines of the others. In contrast, our approach enables us to address how, on average, species with specific traits respond to disturbance of various types.

2. Methods

2.1. Choice of studies

Our analysis included 19 studies from throughout the world (Fig. 1, Appendix A). In all cases, the disturbance studied was associated with humans and the response was of populations and communities of bees. Data sets were obtained based on a search of published studies and also from individuals willing to share data, over 90% of it from published work. Our analysis required species-level abundance data associated with discrete disturbance types. Some studies estimated abundance from sampled specimens, others recorded visitation rates to flowers. Because methods were consistent among all sites within a study each metric provides an unbiased assessment of disturbance effect. We refer to abundance throughout the paper. Taxonomic identities of all bee species were required so that we could associate specific life-history data to disturbance type. We included only data sets for which sampling method and effort was standardized and consistent among all levels of disturbance.

2.2. Disturbance classification

Five types of non-exclusive disturbance were evaluated, habitat fragmentation/loss, agricultural intensification, pesticide use, tillage, and fire. For most studies we used the categories identified by the original authors. For some studies, the disturbance categories of the original authors were simplified so that they could be included with others in our comparisons. In all cases these designations were made a priori and by individuals who did not carry out the analysis. For example, six agro-forestry categories identified by Klein et al. (2002) were re-categorized to high, medium, and low based on discussion with the lead author. Habitat loss/fragmentation was coded in two ways, depending on the metrics presented by the original authors: (1) as isolation which was measured as the distance to the nearest patch of natural or semi-natural habitat as defined in the original studies, or (2) the proportion of natural or semi-natural habitat surrounding the study sites based on the radius used in the original study. Thus the spatial scale at which fragmentation was assessed varied among studies.

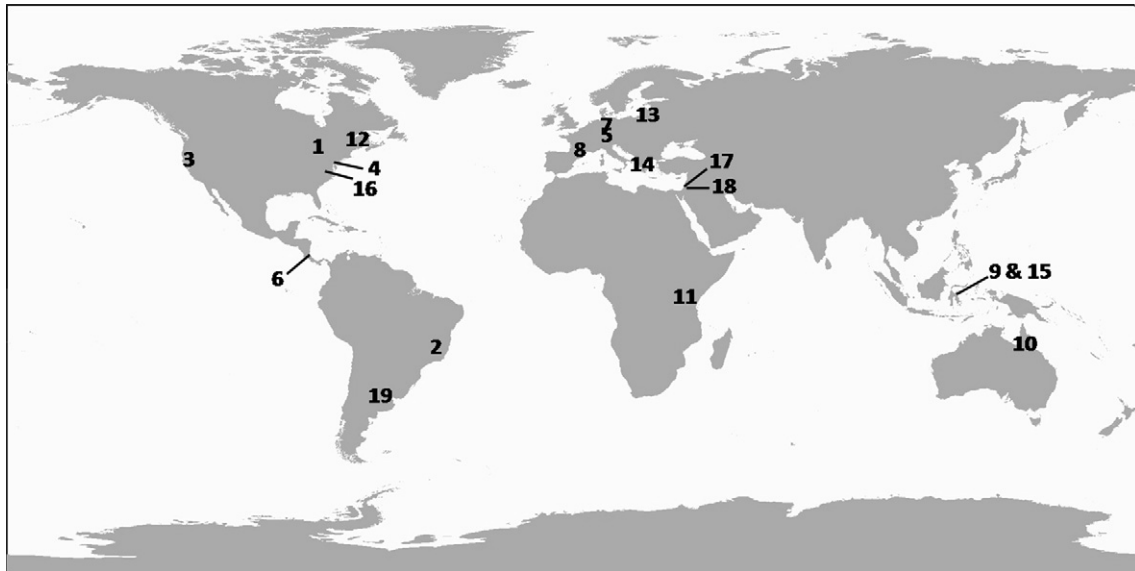


Fig. 1. Map of studies included in our analysis. Numbers correspond to those in Appendix A, which contains study details.

We analyzed the effects of agricultural intensification, first, by coding intensification for the most and least disturbed level within each study, and second, by comparing effects of tilling and spraying explicitly. We coded tillage as tilled vs. no-till farming (e.g., Shuler et al., 2005) and pesticide use as farms that used only inorganic pesticides (high) vs. farms that either used organic or no pesticides (low). We used two separate comparisons for analyzing fire impacts based on the time since the burn event: unburned vs. recent (<5 years old) and old (>20 years) burns. Vegetation succession and other factors are likely to make recent vs. older burned sites very different habitats for pollinators (Moretti et al., 2009).

To test bee response generally to disturbance of all types, we first categorized each site in each study as relatively disturbed or undisturbed, and compared how each ecological and life-history trait affected the response of bee species to disturbance. In each disturbance category, the “disturbed” vs. “un-disturbed” sites were as follows: most isolated vs. closest to natural habitat, relatively intensive vs. organic or less-intensive agricultural management, high pesticide inputs vs. organic or no-spray, tilled vs. no-till, burned vs. unburned, suburban vs. rural (Zanette et al., 2005; Winfree et al., 2007), landfill or garbage dump vs. native vegetation (Rust et al., 2003; Kelly et al. unpublished) and grazed vs. ungrazed temperate forest (Vazquez and Simberloff, 2002, 2003).

2.3. Traits

To explore the effect of life-history and ecological traits (hereafter referred to as traits) on bee responses to different types of disturbance, we compiled life-history and ecological data for all species reported in each study. Among all studies, this effort included 613 bee taxa excluding cleptoparasites. Cleptoparasites were excluded because major traits such as nest location, nest construction and trophic specialization are dictated by their hosts. Cleptoparasite responses are thus not independent of those of their hosts. From these data we considered five traits that varied among bees, that might result in differential responses to any of our disturbance variables, and that were assignable to all or most bees in the various datasets. Prior to analysis we reduced the number of character states for each trait to allow more species and studies to be included in the analysis (Table 1, Appendix B).

Table 1
Traits and character states used in analyses.

Trait	States	Definition
Body size	Continuous	Measured as inter-tegular-distance (ITD) the distance between the nearest edges of the tegulae (plates covering the wing bases). Only data for females were used in final analysis. ^a
Nest location	Above ground Below ground	Above ground species included all nest types, from cavity nests like those of the honey bee to tunnels burrowed into wood.
Nest construction	Rent Excavate	Renters construct nests within existing tunnels or other cavities regardless of nest location. Excavators dig or bore the chamber/tunnel within existing substrate.
Lecty	Specialists = oligoleges Generalists = polyleges	Trophic specialization defined by the range of pollen species collected by females and consumed by offspring. See Appendix B for complete description.
Sociality	Solitary Social	Social species included eusocial as well as semi-social species. Others were considered solitary.

^a Inter-tegular measurements for bumble bees were based on samples of workers.

We estimated body size by measuring inter-tegular distance (ITD) from pinned specimens (Cane, 1987) and used this metric in analysis. Information on other traits was compiled from the primary literature, from the Catalogue of Hymenoptera (Krombein et al., 1979) or from Bees of the World (Michener, 2000). If published data were unavailable, we relied on a consensus of expert opinion or inferred trait data based on phylogeny (e.g., all species of *Lasiglossum* (*Evylaeus*) nest below ground). Species were dropped from the analysis where traits could not be assigned unambiguously (Table 3 provides final sample sizes for individual analyses). All traits were assigned based on data independent of the studies included in our analysis.

2.4. Analyses

We analyzed relationships between bee traits, disturbance and bee abundance using generalized linear mixed-effects models. Following Ricketts et al. (2008), models were of the general form $E(A) = e^{\beta_0} e^{\beta X} \rightarrow \ln[E(A)] = \beta_0 + \beta X$, where $E(A)$ refers to the expected abundance of each species in each treatment, β are the regression coefficients, and X the predictor variables. In general, the exponential relationship means coefficients refer to proportional changes in abundance, which allowed us to account for differences in units among the studies (see Ricketts et al., 2008). Because abundance was 0 for some species in either the disturbed or undisturbed state, we $\ln[A + 0.5]$ transformed abundance variables, so the exponential relationship is approximate. Residuals of fitted models were visually inspected, and all were approximately normal, i.e., unimodal and symmetric. All analyses were performed in R v.2.7.0 software (R Development Core Team, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna (2004). R Development Core Team, 2004).

We first fit models without bee traits to estimate the overall effects of each disturbance type on bee abundance for all disturbance types that were represented in at least three studies. Isolation was coded as distance from natural/semi-natural habitat, loss of semi-natural habitat was examined as the proportion non-natural (0 = 100% natural, 1 = 0% natural) surrounding the study site, and categorical disturbance variables were coded 0 for the less disturbed category (e.g., less intensive farming, unburned, untilled, low-pesticide), and 1 for the more disturbed category. In addition to disturbance (a fixed effect), these models included study as a fixed effect (to account for different sampling units across studies; Ricketts et al., 2008), and the disturbance \times study interaction, site nested within study, and bee species as random effects. The disturbance \times study term accounted for the expected random variation in the effect of disturbances among studies. The site-within-study random effect accounted for expected differences in abundance of species at different sampling locations. The species effect was included to account for species-associated variation that might have masked interpretation of the traits of interest. By using a random effect we acknowledge that species responses to disturbance will vary in some unknown way rather than focusing on mean effects of a species for each study, which is not the goal of our paper. In 57 of 613 taxa were reported to morpho-species rather than to species; we refer to these as species throughout. Morpho-species were only included if traits could be assigned unambiguously. Individual records in the analysis were abundances of each bee species, so the coefficients describing effects of disturbance are interpreted as the average proportional change in abundance among species. Thus, we weighted rare and common species equally because we were interested in estimating the influence of particular traits on species' responses.

We tested whether life-history and ecological traits mediated bee responses to each disturbance type by modifying the above models to include trait as a new predictor variable and the interactions between traits and disturbance. A significant effect of life-history or ecological trait on bee responses to a particular disturbance is indicated by a significant interaction coefficient in the model. We were not able to obtain data on every trait for each species, so we could not look at traits simultaneously in multiple regression or other multivariate analyses. Therefore, we analyzed effects of each trait, in turn, in separate models including all species for which we had data for the trait of interest. We calculated the correlation between pairs of traits across species and all studies as a rough measure of the extent to which these traits can be evaluated independently in our data base (Table 2). For example, perfect correlation between above-ground nesting and sociality would indicate that all species that nested above ground were also social. In

Table 2

Correlations between life-history traits across taxa, with bootstrapped P -values, and N = number of pair-wise complete observations for each test.

Traits		Correlation	P -value	N
Female ITD	Above	0.128	0.039	271
Female ITD	Rent	0.101	0.112	270
Female ITD	Social	0.008	0.900	285
Female ITD	Oligolectic	-0.053	0.440	245
Above	Rent	0.731	<0.001	429
Above	Social	0.001	0.987	428
Above	Oligolectic	-0.143	0.013	303
Rent	Social	0.301	<0.001	416
Rent	Oligolectic	-0.094	0.105	295
Social	Oligolectic	-0.245	<0.001	296

Female ITD = body size, Above = nests made above ground, Rent = nests occupy existing cavities or holes.

our data set, renting significantly correlated with nesting above ground, and with sociality; therefore, interpretation of renting in our final analysis should be interpreted in parallel with nest location. Similarly, there was a strong tendency for specialist species to be solitary, so we cannot unambiguously separate these trait effects.

In agricultural landscapes worldwide, honey bees (*Apis mellifera*) are often managed for crop pollination. More colonies are used in areas with more intensive agriculture; thus, the presence of honey bees might diminish our ability to detect the role of traits held by honey bees on the general response of all bees to disturbance. For example social species other than honey bees might respond negatively to more intensive agriculture, but with honey bees included in the analysis the effect of sociality on response might be nullified. To test whether the observed responses of bees in agricultural landscapes could be due to managed honey bees, we re-ran tests of isolation, agricultural intensity, tilling and pesticide use excluding *A. mellifera*. The effect of removal on the outcome of analysis might also depend on dominance of honey bee records in the analysis. For example, if honey bees composed 50% of the records for above-ground nesting species in an analysis, removing them would likely produce a greater change in outcome than if they represented only 2% of such records. We therefore also looked for a relation between proportion of records that were honey bees and the magnitude of change in the coefficient. We did not find such an effect consistently in the data set.

3. Results

From all studies we included 613 total bee species, 159 nested above ground and 307 below ground, 125 were renters and 329 excavators, 362 were generalists and 37 specialists, and 90 were social and 414 solitary.

Among all species and all disturbances, bees tended to be less abundant in disturbed areas (Table 3, All disturbances). The specific disturbance types we examined all tended to decrease the abundance of bees (Table 3, Main effects column), although when all species were analyzed together only the effect of isolation on abundance was marginally statistically significant ($P < 0.10$). Bee abundance tended to decline noticeably but non-significantly in areas with higher-intensity agriculture (Table 3, agriculture intensity, pesticide use). However, responses to proportion natural habitat in the landscape and to tilling were variable among bee species.

As expected, this substantial variation in response to disturbance among species partly reflects significant differences in response among species with different life-history or ecological traits. Across all disturbances, abundances of above-ground-nesting species were, on average, six times more reduced by

Table 3
Effects of different disturbances on bee abundance (main effect) and effect of life-history traits on bee responses to these disturbances.

Disturbance	Life-history traits										
	Main effects					Body size (mm)					
	nS	Coef. ^a	SE	χ^2	P	nT	Coef.	SE	χ^2	P	nT
All disturbances	19	-0.19	0.11	3.3	0.068	613	0.04	0.05	0.9	0.352	333
Isolation (km)	6	-0.41	0.21	3.3	0.068	79	0.26	0.15	2.9	0.087	40
Proportion natural habitat	3	-0.33	0.87	0.0	>0.999	183	-0.07	0.10	0.6	0.441	133
Agricultural intensity	8	-0.19	0.16	1.2	0.264	314	-0.03	0.10	0.1	0.758	191
Pesticide use	6	-0.22	0.17	1.7	0.196	155	0.66	1.08	0.0	>0.999	79
Tilled fields	7	-0.12	0.36	0.0	>0.999	161	-0.22	0.51	0.2	0.672	83
Fire-old	3	-0.06	0.13	1.5	0.223	138	0.15	0.12	1.7	0.198	66
Fire-recent	3	-0.07	0.34	0.1	0.771	138	-0.09	0.12	0.6	0.447	66

Disturbance	Nesting location (1 = above ground, 0 = below)					Nest construction (1 = rent, 0 = construct)				
	Coef.	SE	χ^2	P	nT	Coef.	SE	χ^2	P	nT
	All disturbances	-0.16	0.04	16.6	<0.001	468	-0.18	0.04	20.1	<0.001
Isolation (km)	0.02	0.09	0.1	0.780	61	-0.02	0.06	0.1	0.802	58
Proportion natural habitat	0.06	0.10	0.4	0.511	137	-0.11	0.10	1.1	0.288	138
Agricultural intensity	-0.11	0.08	1.9	0.169	234	-0.04	0.09	0.2	0.629	234
Pesticide use	-0.03	0.22	0.0	>0.999	118	0.09	0.23	0.0	0.879	120
Tilled fields	0.66	0.31	4.2	0.041	124	0.56	0.34	2.5	0.116	126
Fire-old	0.12	0.06	3.7	0.053	105	0.01	0.07	0.0	0.884	101
Fire-recent	-0.06	0.06	1.0	0.306	105	-0.03	0.07	0.1	0.721	101

Disturbance	Sociality (1 = social, 0 = solitary)					Trophic specialization/lecty (1 = oligo, 0 = poly)				
	Coef.	SE	χ^2	P	nT	Coef.	SE	χ^2	P	nT
	All disturbances	-0.09	0.05	4.0	0.047	507	-0.05	0.07	0.6	0.457
Isolation (km)	-0.17	0.08	4.8	0.029	66	-0.01	0.13	0.0	0.911	60
Proportion natural habitat	0.39	0.10	13.9	<0.001	133	-0.26	0.11	5.3	0.022	153
Agricultural intensity	0.20	0.10	3.6	0.056	245	-0.24	0.13	3.6	0.058	211
Pesticide use	-0.81	0.20	15.2	<0.001	133	0.17	0.37	0.6	0.422	82
Tilled fields	0.82	0.31	6.7	0.010	139	-1.81	0.60	9.0	0.003	85
Fire-old	-0.10	0.12	0.8	0.382	119	0.10	0.11	0.8	0.361	44
Fire-recent	0.18	0.11	2.7	0.099	119	-0.19	0.11	1.0	0.308	44

^a Coefficients for main effect of each disturbance and for interactions between disturbance type (rows) and life-history traits (columns). Significant coefficients for interactions (**in bold**) indicate that this trait affected bees response to the specific type of disturbance. Positive coefficient values indicate bee species with the trait coded as 1 are more abundant in disturbed areas. Oligo = oligolectic. nS = # studies, nT = # species (taxa).

disturbance than those of bees nesting below ground (Table 3, Fig. 2A). Likewise renters responded 4.5 times more strongly to disturbance than did excavators (Fig. 2B) and social species 17% more strongly than solitary species (Fig. 2C). In contrast, small-bodied species compared to large-bodied species and specialists compared to generalists did not differ significantly in their overall response to disturbance (Table 3, Fig. 2D and E).

Two traits, nest location and sociality, affected species' responses across multiple disturbance types. Above-ground-nesting species were nine times more strongly affected than below-ground-nesting species by overall agricultural intensification (Fig. 3A). This effect became stronger and significant when honey bees were removed from the analysis (Table 4). If honey bees were removed from the analysis, above-ground nesters also responded more negatively than did below-ground nesters to isolation from semi-natural habitats (Table 4). The abundance of above-ground nesters decreased on average 47% as isolation increased from 0 to 1 km. Below-ground nesters decreased in abundance by 25% over the same distance. Only below-ground nesting bees were strongly affected by tilling (Fig. 3B). Below-ground nesting bees were not significantly affected by fire, whereas above-ground nesters were 15% less abundant after recent burns, and 8% more abundant in sites with older burns, relative to unburned sites (Fig. 3C). Social bee species were more strongly affected than solitary species by isolation and pesticide use (Fig. 4a and b). In response to pesticides, social species showed a 70% reduction in abundance on average compared to a 29% increase by solitary species. In contrast, social species were 3.6 times less affected by overall agricultural intensification and almost 5 times less affected by tilling (Fig. 4). When honey bees were removed from the analysis, the

magnitude of the difference in response to agricultural intensity remained (social species were about 5 times less affected), but the difference was no longer significant probably due in part to reduced power of the analysis (Table 4).

Other traits had a less consistent effect on species responses across disturbance types, but some effects were striking and suggest an underlying mechanism for how the disturbance affects species with particular traits. Small-bodied bee species were affected more strongly than large-bodied bee species to isolation, indicating a role for dispersal capability (Table 3). This effect disappeared if honey bees were removed from the analysis (Table 4). Specialists tended to be more strongly affected than generalists by overall agricultural intensification and tilling, suggesting that suitable floral resources needed by specialists may have been absent or scarce in such conditions (Fig. 5). The effect of tilling was not significant after honey bees were removed from the analysis (Table 4). Renters were more negatively affected than excavators by isolation.

4. Discussion

Across multiple disturbances and taxa, bees generally were less abundant in response to anthropogenic disturbance. This result is consistent with that of a recent meta-analysis of bee response to multiple disturbance types (Winfree et al., 2009), including habitat loss, agricultural intensification, logging, grazing, fire pesticide use and tillage. Like in that study, however, responses to individual disturbance types were modest and showed great variation when pooled among all bee species independent of ecological or life-history traits. Among the diverse study systems and taxa we included

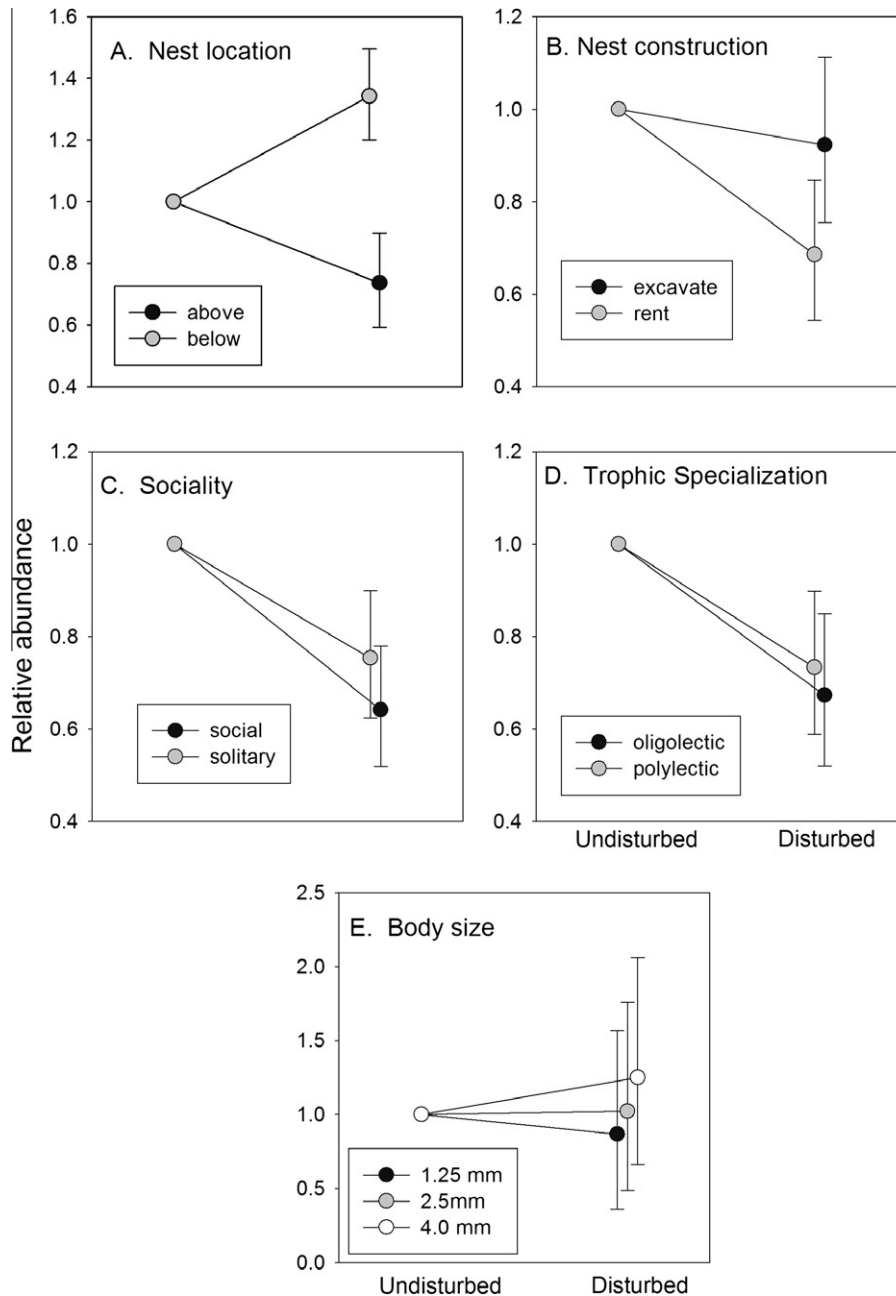


Fig. 2. Mean \pm se relative abundances of species with different ecological and life-history traits in undisturbed and disturbed sites. Means were calculated among all disturbance types. The value for the undisturbed condition is scaled to a mean of one so that disturbed values change relative to this value. Body size response was calculated for inter-tetragonal spans in the smallest middle and largest third of species.

in this study, some traits consistently predicted how bees responded to specific disturbances. These results underscore the predictive power of life-history traits in environmental assessments. The results also allowed us to identify those traits that were relatively uninformative for predicting response to single disturbances and to disturbance in general. This information helps to guide more careful investigation of the links between informative life-history traits, population dynamic variables and the mechanisms by which species interact with their environment.

4.1. Trait-specific effects

Nesting location and sociality were especially predictive, and the associated responses confirmed biologically reasonable expecta-

tions. For example, above-ground nesters were more strongly affected than below-ground nesters by agricultural intensification excluding tillage. Most species that build nests above-ground construct them in perennial grass, forb or shrub stems, or in dead wood that would tend to be removed by more intensive agricultural practices. As a result, nesting substrates for these species are limited through intensification whereas suitable substrate for ground-nesting species, such as in soil at field margins and in fields themselves (Mathewson, 1968; Kim et al., 2006), is available throughout agriculturally dominated landscapes. The parallel result for isolation from natural or semi-natural habitat is likely driven by the same mechanisms and makes sense given that all studies of isolation that we included were carried out in agricultural landscapes. The contrasting response by above-ground-nesting species to tillage

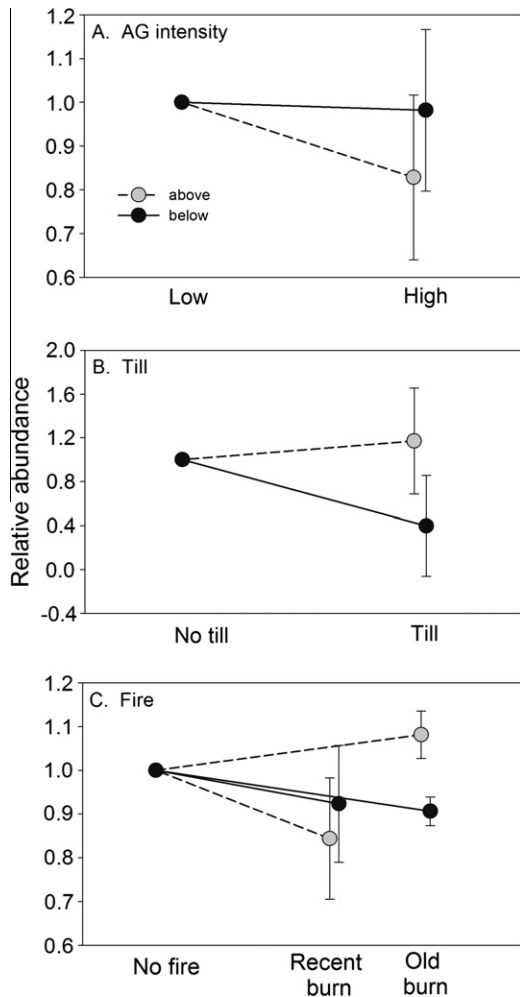


Fig. 3. Mean \pm se relative abundance of above ground vs. below-ground nesting bee species at less and more disturbed sites for different categories of disturbance, (A) agricultural intensity, (B) tilling (C) fires including recent and old burns. The value for the undisturbed condition is scaled to a mean of one so that disturbed values show changes relative to this value. Standard errors include error for mean response (or slope) and interaction whereas significance testing was based on interaction terms from the general linear models therefore error bars are large compared to significance test results. See coefficients and *p*-values for life history \times disturbance interaction terms in Table 3.

underscores the importance of nest location as a key response trait. Tilling directly kills bees that nest near the soil surface (Shuler et al., 2005); however, whether or not a farm tills is unlikely to affect the availability of nest substrates for bees that nest above ground.

Above and below-ground nesters also responded differently to fire and their responses depended on the time since the burn

(Fig. 3C). Species that nested above ground were more negatively affected by recent burns, probably because this disturbance destroys their nests and may not do so for species that nest in the ground (Potts et al., 2005). Furthermore, fires tend to remove old dead wood immediately, but may soon allow many perennial shrubs (e.g., *Rubus* and *Asphodelus* spp.) to become established which provide nesting substrates for aerial nesters and create new dead wood that would become available for various species nesting above ground as this wood decomposes (Stockhammer, 1966). This rebound effect of available nest sites may explain why the average abundance of above-ground nesters was positively affected by habitat changes occurring as a result of burns that occurred more than 5 years previously. In contrast, bee species that nested below ground were more negatively affected by older burns than above-ground-nesting species, perhaps because flushes of new vegetation following fires lead to dense herbaceous and shrub growth (Potts et al., 2003a, 2005) that in older burned areas may reduce access to unvegetated patches used by ground-nesters. Thus, the differences in response between above- and below-ground nesters are consistent with temporal dynamics in the availability of nest resources. Results of our analysis are consistent with other recent work that focuses on fires and documents substantial shifts in the representation of different traits within communities (Moretti et al., 2009); however the direction of the shift in that study, toward above-ground, cavity-nesting species, contrasts with the pattern we found. The differences may reflect fundamentally different ways of testing the data related to different goals of the studies (i.e., pooled abundances within a guild vs. species-level analysis, see Section 1). Other studies have highlighted the importance of nest location/substrate and the link between available nest sites and populations of certain bee species (Potts and Willmer, 1997, 1998; Cane et al., 2006).

Sociality predictably affected bees' response to disturbance overall and to several specific types. This result largely parallels other recent analyses of bee responses that have considered life-history effects and used data from multiple study systems (Ricketts et al., 2008; Winfree et al., 2009). The stronger response of social species to isolation from natural habitat that we found has been attributed to correlated differences in nesting substrate and nest location (Ricketts et al., 2008; Winfree et al., 2009). Tropical social species, including honey bees, most often build nests associated with forest trees, which are not present in agricultural habitat. Some temperate social species, namely bumble bees, nest in existing cavities and although these substrates are available in certain disturbed landscapes they are not common in intensively cultivated areas (Osborne et al., 2008). The lack of response to agricultural intensification likely reflects a more complex set of variables involved including tillage and pesticide use and also the interaction of sociality with other bee traits. Social species were more strongly affected than were solitary species by tilling and pesticide use within agricultural landscapes. It is unclear why sociality itself

Table 4

Coefficients for interaction between life-history trait and disturbance type. Analyses were run including *Apis mellifera* and without *A. mellifera* (*no Apis*).

Disturbance	Nest location		Body size (mm)		Lecty		Nest construction		Sociality	
	Coef.	<i>P</i>	Coef.	<i>P</i>	Coef.	<i>P</i>	Coef.	<i>P</i>	Coef.	<i>P</i>
Isolation (km)	0.02	0.78	0.26	0.09	-0.01	0.91	-0.02	0.80	-0.17	0.03
Isolation (km) <i>no Apis</i>	-0.27	0.01	0.06	0.70	0.03	0.83	-0.19	0.00	-0.28	<0.001
Agricultural intensification	-0.11	0.17	-0.03	0.76	-0.24	0.06	-0.04	0.63	0.20	0.06
Ag intensification <i>no Apis</i>	-0.17	0.03	-0.02	0.79	-0.25	0.04	-0.09	0.27	0.16	0.12
Pesticide use	-0.03	>0.999	0.66	>0.999	0.17	0.42	0.09	0.88	-0.81	<0.001
Pesticide use <i>no Apis</i>	-0.12	>0.999	0.88	0.45	-0.14	>0.999	0.10	0.77	-0.89	<0.001
Tillage	0.66	0.04	-0.22	0.67	-1.81	0.00	0.56	0.12	0.82	0.01
Tillage <i>no Apis</i>	-0.15	0.65	-0.63	0.09	-0.43	0.48	-0.24	0.51	0.73	0.01

Note: Values (in bold) indicate statistically significant changes in the outcome of the analysis with and without inclusion of *A. mellifera*. For trait descriptions refer to Table 1.

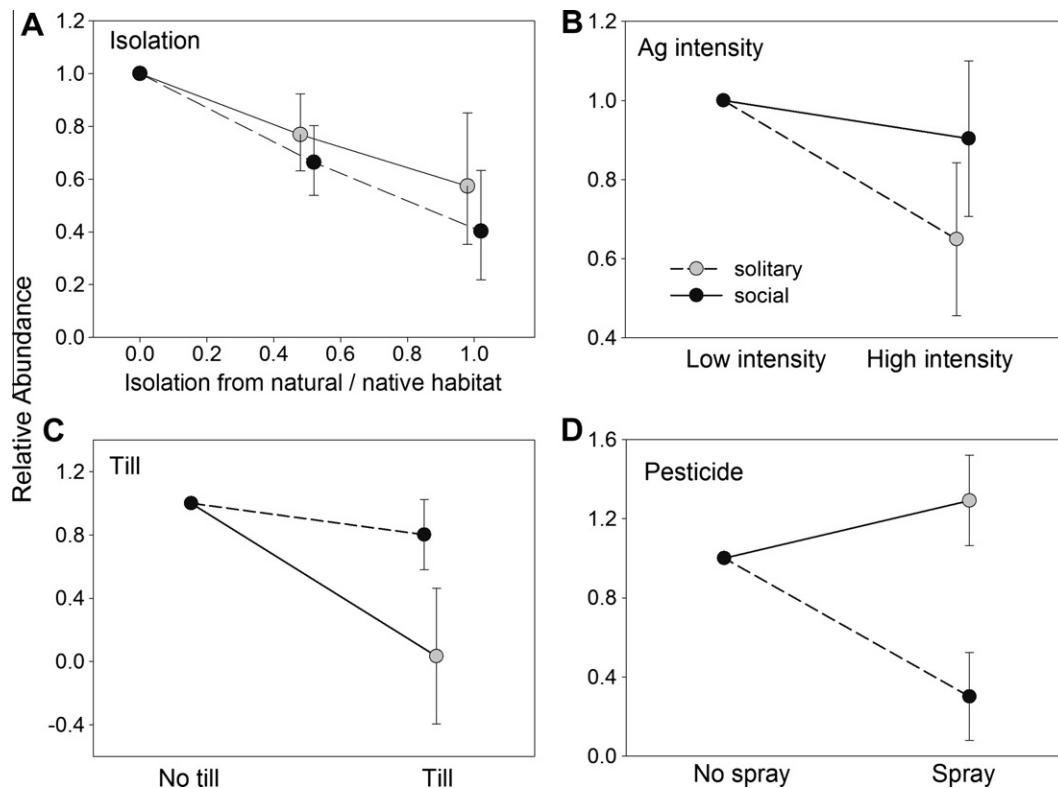


Fig. 4. Mean responses of social and solitary species to different disturbances, (A) isolation from semi-natural habitat, (B) agricultural intensity (C) tillage (D) pesticide use. Values are mean \pm se relative abundance among species at disturbed and undisturbed sites. Mean for the less disturbed condition is scaled to 1 so that disturbed values show changes relative to this value. Standard errors include error for mean response (or slope) and interaction whereas significance testing was based on interaction terms from the general linear models therefore error bars are large compared to significance test results. See coefficients and *p*-values for life history \times disturbance interaction terms in Table 3.

should affect bees' sensitivity to tilling independent of other traits like the nest location that directly affect response to tilling. Many of the social species included in our analysis were also ground-nesting; however, ground-nesting was not significantly correlated with sociality (Table 2). The greater sensitivity of social species to pesticides matches the effect found by Winfree et al. (2009). Sensitivity of social species may be relatively acute because colonies essentially bioaccumulate pesticides and experience exposure at greater doses for longer periods. This occurs because: (1) foragers return with pollen and nectar that they transfer among individuals through social feeding and incorporate into the nest itself; (2) colonies are active for longer periods than individual solitary females and thus integrate exposure to toxins over more of the active season, (3) queens in particular feed upon resources collected throughout the year – from the fall to late summer, (4) foragers from the same colony visit different floral resources which may lead to contact with toxins over a wider area and from more sources and (5) some species exploit mass flowering crops extensively (Westphal et al., 2003), and recruit to concentrated resources (*Apis* spp.), which then become traps when sprayed. Together these factors may increase total exposure per colony compared to single nests of solitary species.

Of the traits we included, body size showed surprisingly little consistency in its influence on the response of bee species to disturbance. Body size is correlated with foraging flight distance (Gathmann and Tscharrnke, 2002; Greenleaf et al., 2007) and so would be expected to strongly influence the scale over which bees can access resources and their ability to recolonize disturbed sites. Thus, larger species should be less affected by isolation (e.g. Klein et al., 2008), but in our analysis, once honey bees were removed they were not. Body size also negatively correlates with population

size, intrinsic growth rate and temporal fluctuations in population size in some species (Henle et al., 2004), all of which increase sensitivity to habitat loss. Although body size has been identified as important for determining responses to landscape change in other taxa, there are opposing predictions of its effects (Henle et al., 2004) and it is perhaps not surprising that we too found no clear overall effect. Small-bodied species also require fewer resources to produce offspring than do large-bodied species and so may be better able to maintain population sizes in disturbed or degraded habitats. Such an effect might counteract the reduced recolonization ability of smaller-bodied species. Other recent studies of the effect of body size on response of bees to fragmentation and habitat loss have contrasting results (Cane et al., 2006; Winfree et al., 2007; Klein et al., 2008).

4.2. Trait correlations and variable response

In this study, we analyzed each trait separately as though it was not constrained by other traits in the analysis when, in reality, species represent mosaics of traits that are not biologically independent. We chose this approach because not all traits were available for all taxa, and analyzing trait pairs in combination would have substantially reduced sample size for many analyses. Nonetheless, we acknowledge that variation in one trait among species may reduce the mean effect of another trait on response to disturbance. For example, large-bodied species may be trophic generalists or specialists, nest above-ground or below-ground, and be solitary or social. In a study of urban fragmentation, Cane et al. (2006) found that trophic specialist bees generally declined more strongly than trophic generalist bees as fragment size decreased; however, the only trophic specialist that nested

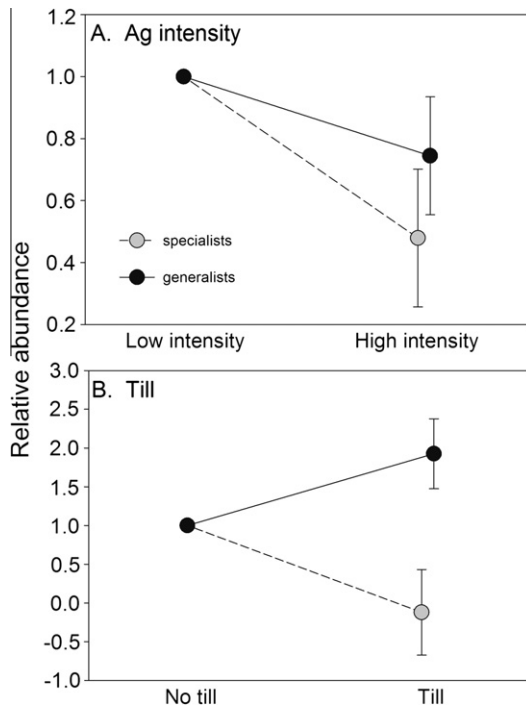


Fig. 5. Mean \pm se relative abundance of trophic specialists vs. trophic generalists at less and more disturbed sites for different categories of disturbance, (A) agricultural intensity (B) tillage. Mean for the less disturbed condition is scaled to 1 so that disturbed values show changes relative to this value. Standard errors include error for mean response and interaction whereas significance testing was based on interaction terms from the general linear models therefore error bars are large compared to significance test results. See coefficients and *p*-values for life history \times disturbance interaction terms in Table 3.

above-ground in cavities was much more abundant in urban fragments, suggesting that nest site availability in undisturbed desert was a greater constraint to population density for this species than food resources. Similarly, correlation among traits could also reduce the mean effect among species if the traits acted in contradictory ways. For example, a potentially positive effect of body size on response to disturbance might have been masked by its correlation with nest location (Table 2). Although larger more mobile species were predicted to respond less to isolation, larger species tended to nest above ground, and species with the latter trait were more affected by isolation. The interaction among life-history traits can be critical for understanding species responses to disturbance (Davies et al., 2004). Such potential interactions have also led some authors to examine community responses using multivariate methods to form guilds with shared trait clusters (Kolb and Diekmann, 2005; Moretti et al., 2009). As studies and data on bee life-history traits become increasingly available, we encourage researchers to build on our results by exploring joint effects and interactions of multiple traits.

Just as with bee traits, there was also non-independence among some types of disturbance we investigated. Agricultural intensification involves changes in local management and also removes natural habitat from the landscape (Tscharntke et al., 2005; Kremen et al., 2007). Like for life-history traits, if disturbances have contradictory effects on species with a specific life-history trait, interactions between them could reduce mean response or inflate variability in response among species. The effect of habitat fragmentation on species with low dispersal (such as small bees) is less dramatic if fragmentation does not degrade the quality of remaining habitat (Poschlod et al., 1998; Oostermeijer, 2000). In this case and perhaps more generally, interaction among disturbances may lead to more complex responses of ecological/life-history groups.

For the above example with species mobility, intermediate-sized species or those with moderate mobility, would be most sensitive to certain disturbances and the smallest and largest species more robust. In addition disturbances may act in non-linear ways over a range of intensity or spatial scale, which also could increase the variance in average response measured among studies. In a meta-analysis, Winfree et al. (2009) found that severe fragmentation negatively affected bees but moderate levels of disturbance either had a positive effect or none at all.

The large variance as well as modest mean effects we saw for some species traits and disturbances could potentially arise from pooling data from biogeographic regions that differ in species composition and distribution of traits among species. Such differences might arise because of historical biogeography, phylogeny or environmental conditions that preclude species with certain traits from occurring there, so-called species sorting (Ricklefs, 2004). We avoid some confounding regional effects because most of the data sets we used (24 of 36 individual comparisons among 19 data sets) recorded species abundance at “disturbed” and “un-disturbed” sites within the same study area. If pooling among geographic regions was a hidden influence in our analysis it is all the more striking that we found consistent effects for some traits over all regions. Explicit testing of how region-specific effects of traits and the relationships among species influence bee community response to disturbance will require larger data sets and is an exciting goal for the future.

5. Conclusions

Despite the variability in responses of bees with shared life-history traits, our results suggest that life-history and ecological traits can be used to predict bee responses to a variety of disturbance types. To an extent, species formed trait groups with shared responses. Because bees are the dominant pollinators of wild plant populations and crops worldwide there is growing concern about declines of their populations. We have demonstrated that species traits can be used to inform management practices relevant to bees. These practices relate to features of the habitat or resources that would mitigate negative impacts of disturbances upon bees. For example, in intensive agricultural habitats, including nesting substrates for bees that nest above ground in wood and twigs could help to stabilize populations. Because certain traits consistently affect species responses to different disturbance types, pollinator communities are likely to exhibit shifts in functional group composition in response to environmental change. Such shifts in functional groups would produce complex non-linear responses of pollination services compared to random loss of pollinator species (Klein et al., 2008). Our results and their implication for changes in ecological communities and ecological function suggest that a shift of focus from indicator species to indicator traits, or at least inclusion of indicator traits would be useful for conservation purposes. The inclusion of life-history traits in determining pollinator responses to landscape change also may help to explain variable responses among broader taxonomic groups (Jauker et al., 2009).

There is a long history of comparing species with different ecological traits in communities and asking how they respond to specific cases of habitat turnover or to disturbance. The terms guild and functional response group stem from this tradition. This study is novel because we incorporated a range of ecological traits and disturbance types from communities worldwide to investigate whether we could predict species' response to disturbance. That we were successful in this despite the considerable variance in the data used in our analysis adds considerable generality to these kinds of approaches.

Acknowledgements

This paper was prepared as part of NCEAS working group “Restoring an ecosystem service to degraded landscapes: native bees and crop pollination” organized by NMW and C. Kremen and funded by NSF Grant DEB-0072909. We thank our co participants in the working group. S. Cunningham, I. Steffan-Dewenter, A.-M. Klein, R. Winfree, D. Vazquez, B. Gemmill-Herren provided additional data on bee abundance from their published work. Some data on bee life-history traits were provided by T. Griswold and F. Vivallo and S. Roberts. The Natural History Museum, London, UK and Smithsonian Institution, Washington DC, USA provided access to some bee specimens from which we assessed body size. L. Scullo helped measure some of the bees used in our analyses. R. Winfree provided valuable comments on the manuscript. SGP was also supported by the Integrated Project ALARM (Assessing Large-scale environmental Risks for biodiversity with tested Methods, www.alarmproject.net) within the European Union’s Sixth Framework Program (Contract Number: GOCE-CT-2003-506675).

Appendix A

See Table A1.

Appendix B

Trait categorization for bees. Description of each trait with explanation of its purported role in response to environmental dis-

turbance. Explanation of how original character states were collapsed for final analyses.

All discrete variables were collapsed into binary categories to simplify interpretation.

1. *Body size*: continuous metric based on inter-tegular span (Cane, 1987; Greenleaf et al., 2007). This measure correlates very strongly with other measures of body size and captures the volume of the thorax which contains the flight muscles. Measures were averaged on up to 10 individuals of male and female for each species, unless all data in the study involved a single sex or caste (e.g., *Apis mellifera* workers). For *Bombus* spp. we separately measured workers queens and males. Final analysis was constructed on measurements for workers.
2. *Nest location*: initially locations were categorized as above-ground nesting in stems, above-ground nesting in wood and below-ground. The distinction in above ground would allow for separation of species that depend on substantial woody material, such as branches and logs vs. those that could nest in more ephemeral types of above ground vegetation, like grass and forb stems. Categories were collapsed to above vs. below ground to increase sample size and provide greater generality.
3. *Nest construction*: this trait included rent for species that nest in existing holes or cavities either above or below ground; construct for species that build the nest exterior (envelop) and cells de novo using collected materials, and excavate for species that bore the tunnel/cavity in which the brood cells are constructed.
4. *Trophic specialization*: this categorization was based on specialization for pollen collection (lecty). Categories included narrow oligolecty, broad oligolecty, and polylecty (see Cane and Sipes, 2006). These categories were collapsed to oligolectic (which included narrow or broad) vs. polylectic. Our goal was to separate species whose narrow floral host range would make them more susceptible to anthropogenic disturbance vs. species that were likely to be able to easily shift to alternative host plants.

The following traits were also assigned to each species, but were not included in our analysis. Several of these traits could be used to assess changes in pollination functional groups.

1. *Reproductive strategy*: free living vs. cleptoparasitic.
2. *Pollen carriage location*: pollen carried externally, pollen carried internally.
3. *Consistency of transported pollen*: pollen transported dry, pollen transported.
4. *Extraneous nest material*: types of non-food resources, plant soil, resins, etc. collected in order to construct the nest.
5. *Voltinism*: number of generations produced within a single growing season.
6. *Flight season*: start and end.

References

- Antonini, Y., Martins, R.P., 2003. The flower-visiting bees at the ecological station of the Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil. *Neotropical Entomology* 32, 565–575.
- Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T., Wilson, W.G., 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85, 2408–2421.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354.
- Blanche, K.R., Ludwig, J.A., Cunningham, S.A., 2006. Proximity to rainforest enhances pollination and fruit set in orchards. *Journal of Applied Ecology* 43, 1182–1187.
- Burd, M., 1994. Bateman principle and plant reproduction – the role of pollen limitation in fruit and seed set. *Botanical Review* 60, 83–139.
- Cane, J.H., 1987. Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society* 60, 145–147.

Table A1

Table of studies used the analysis.

Study #	Citation	Disturbance class	Region
1	Kelly (unpublished thesis)	Disturbance	Eastern NA
2	Antonini and Martins (2003)	Disturbance	South America
3	Kremen et al. (2002)	Landscape, isolation, Ag, pesticide	Western NA
4	Winfree et al. (2007)	Landscape, isolation, Ag	Eastern NA
5	Winfree et al. (2007)	Landscape	Eastern NA
5	Steffan-Dewenter et al. (2002)	Landscape	Western Europe
6	Ricketts (2004)	Isolation	Central America
7	Steffan-Dewenter and Tschardt (1999)	Isolation	Western Europe
8	Rust et al. (2003)	Disturbance, urban	Western Europe
9	Klein et al. (2003a,b)	Isolation, Ag	Indonesia
10	Blanche et al. (2006)	Isolation, till	Australia
11	Gemmill-Herren and Ochieng (2008)	Isolation, till	East Africa
12	MacKenzie and Eickwort (1996)	Ag	Eastern NA
13	Sepp et al. (2004)	Ag, disturbance	Central Europe
14	Potts et al. (2006)	Ag, tillage, pesticide	Mediterranean
15	Klein et al. (2002)	Ag	Indonesia
16	Shuler et al. (2005)	Ag, Tillage, Pesticide	Eastern NA
17	Potts et al. (2003b)	Fire	Mediterranean
18	Potts et al. (2001)	Fire	Mediterranean
14A	Potts et al. (2006)	Fire	Mediterranean
19	Vazquez and Simberloff (2002)	Grazing	South America

NA = North America.

Disturbance = general comparison of more vs. less disturbed sites.

Ag = comparison of higher vs. lower agricultural intensity.

Landscape = proportion of natural/semi-natural habitat within landscape surrounding the site. Full references are found in the main reference list.

- Cane, J.H., Sipes, S., 2006. Floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In: Waser, N.M., Ollerton, J. (Eds.), *Plant-Pollinator Interactions: From Specialization to Generalization*. University of Chicago Press, Chicago, IL, pp. 99–122.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H., Williams, N.M., 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* 16, 632–644.
- Davidson, D.W., Inouye, R.S., Brown, J.H., 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* 65, 1780–1786.
- Davies, K.F., Margules, C.R., Lawrence, J.F., 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81, 1450–1461.
- Davies, K.F., Margules, C.R., Lawrence, J.F., 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85, 265–271.
- Devicor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117, 507–514.
- Fagan, W.F., Meir, E., Moore, J.L., 1999. Variation thresholds for extinction and their implications for conservation strategies. *American Naturalist* 154, 510–520.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16, 265–280.
- Gallai, N., Salles, J.M., Settele, J., Vaissiere, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted to pollinator decline. *Ecological Economics* 68, 810–821.
- Gathmann, A., Tschamtkke, T., 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology* 71, 757–764.
- Gels, J.A., Held, D.W., Potter, D.A., 2002. Hazards of insecticides to the bumble bees *Bombus impatiens* (Hymenoptera: Apidae) foraging on flowering white clover in turf. *Ecotoxicology* 95, 722–728.
- Gemmill-Herren, B., Ochieng, A.O., 2008. Role of native bees and natural habitats in eggplant (*Solanum melongena*) pollination in Kenya. *Agriculture Ecosystems & Environment* 127, 31–36.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. *Biological Conservation* 122, 1–8.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C.R., Settele, J., 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13, 207–251.
- Jauker, F., Deikötter, T., Schwarzbach, F., Wolters, V., 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology* 24, 547–555.
- Kim, J., Williams, N.M., Kremen, C., 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*, 79:309–320.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A.A., Marshall, E.J.P., Tschamtkke, T., Verhulst, J.J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B* 276, 903–909.
- Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tschamtkke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology* 16, 1003–1014.
- Klein, A.-M., Steffan-Dewenter, I., Tschamtkke, T., 2003a. Fruit set of highland coffee increases with diversity of pollinating bees. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270, 955–961.
- Klein, A.-M., Steffan-Dewenter, I., Tschamtkke, T., 2003b. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* 40, 837–845.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtkke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences* 274, 303–313.
- Klein, A.-M., Cunningham, S.A., Bos, M., Steffan-Dewenter, I., 2008. Advances in pollination ecology from tropical plantation crops. *Ecology* 89, 935–943.
- Kolb, A., Diekmann, M., 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19, 929–938.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America* 99, 16812–16816.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R.L., Packer, L., Potts, S.G., Roulston, T.H., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L.D., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10, 299–314.
- Krombein, K.V., Hurd, P.D., Smith, D.R., Burks, B.D., 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, DC.
- Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters* 8, 538–547.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545–556.
- MacKenzie, K., Eickwort, G.C., 1996. Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L) in central New York. *Journal of the Kansas Entomological Society* 69, 185–194.
- Mason, N.W.H., Lanoiselee, C., Mouillot, D., Irz, P., Argillier, C., 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia* 153, 441–452.
- Mathewson, J.A., 1968. Nest construction and life history of the Eastern cucurbit bee, *Peponapis pruinosa* (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 41, 255–261.
- McKinney, M.L., 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28, 495–516.
- Michener, C.D., 2000. *Bees of the World*. Johns Hopkins University Press, Baltimore, MD, USA.
- 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. *Journal of Animal Ecology* 78, 98–108.
- NRC-USA, 2007. *Status of Pollinators in North America*. The National Academies Press, Washington, DC, USA.
- Oostermeijer, J.G.B., 2000. Population viability analysis of the rare *Gentiana pneumonanthe*: importance of genetics, demography, and reproductive biology. In: Young, A.G., Clarke, G.M. (Eds.), *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, UK, pp. 313–334.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A., 2008. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology* 47, 784–792.
- Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters* 9, 741–758.
- Pimm, S.L., Diamond, J., Reed, T.M., Russell, G.J., Verner, J., 1993. Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the United States of America* 90, 10871–10875.
- Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S., Bonn, S., 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science* 1, 75–90.
- Potts, S.G., Willmer, P.G., 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground nesting halictine bee. *Ecological Entomology* 22, 319–328.
- Potts, S.G., Willmer, P.G., 1998. Compact housing in built-up areas: spatial positioning of nests in aggregations of a ground-nesting bee. *Ecological Entomology* 23, 427–432.
- Potts, S.G., Dafni, A., Ne'eman, G., 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. *Oikos* 92, 71–80.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., Willmer, P., 2003a. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. *Oikos* 101, 103–112.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S., Willmer, P., 2003b. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84, 2628–2642.
- Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G., Willmer, P., 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* 30, 78–85.
- Potts, S.G., Petanidou, T., Roberts, S., O'Toole, C., Hulbert, A., Willmer, P., 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biological Conservation* 129, 519–529.
- R Development Core Team, 2004. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Ricketts, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology* 18, 1262–1271.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.-M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11, 499–515.
- Roemer, G.W., 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America* 99, 791–796.
- Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation* 141, 417–426.
- Rust, R.W., Vaissiere, B.E., Westrich, P., 2003. Pollinator biodiversity and floral resource use in *Echium elaterium* (Cucurbitaceae) a Mediterranean endemic. *Apidologie* 34, 29–34.
- Sepp, K., Mik, M., Mand, M., Truu, J., 2004. Bumblebee communities as an indicator for landscape monitoring in the agri-environmental programme. *Landscape and Urban Planning* 67, 173–183.
- Settele, J., Poethke, H.J., 1996. Towards demographic vulnerability categories of butterflies. In: Settele, J., Margules, C.R., Poschlod, P., Henle, K. (Eds.), *Species Survival in Fragmented Landscapes*. Kluwer, Dordrecht, pp. 282–289.
- Shuler, R., Roulston, T.H., Farris, G., 2005. Farming practices influence wild pollinator populations on squash and pumpkin. *Journal of Economic Entomology* 98, 790–795.
- Steffan-Dewenter, I., Tschamtkke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121, 432–440.

- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tschardtke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Stockhammer, K.A., 1966. Nesting habits and life cycle of a sweat bee, *Augochlora pura*. *Journal of the Kansas Entomological Society* 39, 157–192.
- Stoks, R., McPeck, M.A., 2003. Predators and life histories shape *Lestes* damselfly assemblages along a freshwater habitat gradient. *Ecology*, 84:1576–1587.
- Tschardtke, T., Klein, A.-M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8, 857–874.
- Vazquez, D.P., Simberloff, D., 2002. Ecological specialization and susceptibility to disturbance: Conjectures and refutations. *American Naturalist* 159, 606–623.
- Vazquez, D.P., Simberloff, D., 2003. Changes in interaction biodiversity induced by an introduced ungulate. *Ecology Letters* 6, 1077–1083.
- Westphal, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6, 961–965.
- Winfree, R., Griswold, T., Kremen, C., 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21, 213–223.
- Winfree, R., Aguilar, R., Vazquez, D.P., LeBuhn, G., Aizen, M.A., 2009. A meta-analysis of bees' response to anthropogenic disturbance. *Ecology* 90, 2068–2076.
- Zanette, L.R.S., Martins, R.P., Riberio, S.P., 2005. Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning* 71, 105–121.
- Zayed, A., Roubik, D.W., Packer, L., 2004. Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271, S9–S12.