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A meta-analysis of bees' responses to anthropogenic disturbance

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Abstract. Pollinators may be declining globally, a matter of concern because animal pollination is required by most of the world's plant species, including many crop plants. Human land use and the loss of native habitats is thought to be an important driver of decline for wild, native pollinators, yet the findings of published studies on this topic have never been quantitatively synthesized. Here we use meta-analysis to synthesize the literature on how bees, the most important group of pollinators, are affected by human disturbances such as habitat loss, grazing, logging, and agriculture. We obtained 130 effect sizes from 54 published studies recording bee abundance and/or species richness as a function of human disturbance. Both bee abundance and species richness were significantly, negatively affected by disturbance. However, the magnitude of the effects was not large. Furthermore, the only disturbance type showing a significant negative effect, habitat loss and fragmentation, was statistically significant only in systems where very little natural habitat remains. Therefore, it would be premature to draw conclusions about habitat loss having caused global pollinator decline without first assessing the extent to which the existing studies represent the status of global ecosystems. Future pollinator declines seem likely given forecasts of increasing land-use change.

Key words: Apis mellifera; *bee abundance; bee species richness;* Bombus; *ecosystem service; global change; habitat loss; land-use change; meta-analysis; pollination; pollinator; pollinator decline.*

Introduction

Pollinators are a critical component of natural ecosystems because the majority of the world's plant species rely on animal pollinators for sexual reproduction (Linder 1998). Pollination by animals is also an important ecosystem service: 35% of the global plant-based food supply comes from crops that benefit from animal pollination (Klein et al. 2007). There is concern that pollinators may be declining at a global scale (Buchmann and Nabhan 1996, Kearns et al. 1998, NRC 2007), but our understanding of potential declines is limited by a lack of long-term data on population trends (Williams et al. 2001, Ghazoul 2005*a*). These limitations notwithstanding, European pollinator monitoring programs have found significant declines in pollinators as well as the plants they pollinate (Biesmeijer et al. 2006, NRC 2007). Although pollinators have been monitored less intensively outside of Europe (but see Roubik 2001), declines of some prominent taxa have been documented. For example, several North American bumble bee (*Bombus*) species are undergoing such steep declines that they are largely absent from much of their former range (NRC 2007).

Human disturbance, particularly the loss of natural and semi-natural habitats, is regarded as a primary cause of pollinator decline (Kearns et al. 1998, Aizen and Feinsinger 2003, Goulson et al. 2008). The negative effect of habitat loss on biodiversity in general is well documented (Fahrig 2003) and acts through a variety of mechanisms that decrease reproduction and survival. These mechanisms include the loss of forage and

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breeding habitat, population subdivision and the resultant demographic and genetic stochasticity, and disruptions in behavior and interspecific interactions (Fischer and Lindenmayer 2007). Our meta-analysis focuses on bees, which are the primary pollinators of both wild plants and crops (Aizen and Feinsinger 2003, Klein et al. 2007). Until recently there had been little research on how bees are affected by habitat loss, with previous reviews finding fewer than 10 such studies (Cane 2001, Aizen and Feinsinger 2003). Since that time research has accumulated rapidly, but there has been no quantitative synthesis of this growing literature. One might expect bees to be negatively affected by habitat loss as is the case for many better-studied taxa (Fischer and Lindenmayer 2007). In addition, the pollination and reproduction of animal-pollinated plants is negatively affected by habitat loss, suggesting that pollinators are negatively affected as well (Aguilar et al. 2006). On the other hand, many bee species are associated with open habitats (Klemm 1996) and due to their small body size might benefit from even small habitat fragments (Tscharntke et al. 2002). Furthermore, because different habitat types can provide the complementary resources bees need to complete their life cycle (Westrich 1996, Fahrig 2003), some bees might persist or even thrive in moderately human-disturbed landscapes.

Declines in the primary managed crop pollinator, the Western honey bee (*Apis mellifera*), have emphasized the need to better understand native bee ecology and conservation. Over the past few decades, managed honey bee populations in the United States have been reduced by 58% due to parasites, disease, and other problems (NRC 2007). Since 2006, honey bees have been affected by a new and as yet unexplained syndrome termed "colony collapse disorder," raising concern about the sustainability of an agricultural pollination system that relies almost exclusively on a single bee species (Cox-Foster et al. 2007, Stokstad 2007). There are at least 17 000 other bee species globally (Michener 2000) and many of these are known to pollinate crops, either in situ as an ecosystem service (Ricketts et al. 2008), or potentially as managed species (Kevan et al. 1990).

In this paper we use meta-analysis techniques to review and synthesize the published literature on how bee abundance and species richness are affected by human disturbance. We address the following questions: (1) Do different forms of anthropogenic disturbance affect bees similarly? (2) Do results differ between more- and less-disturbed study systems? (3) Is there variation among bee taxa in their response to disturbance? (4) Do social and solitary bees exhibit different responses to disturbance? (5) Are the bee fauna of different biomes differently affected by disturbance? We performed separate analyses for unmanaged wild species, and for honey bees. Although these meta-analyses are based on studies conducted at local and regional scales, strong negative trends in bee abundance and richness with increasing human disturbance might be indicative of a more widespread global decline.

Methods

Literature search

To identify published studies of how pollinators respond to anthropogenic disturbance, we conducted an ISI Web of Science search covering the time period from 1945 to March 2007 using the following search terms: (pollinator* OR bee OR bees OR Apoidea OR pollinat*) AND (fragmentation OR disturbance OR perturbation OR grazing OR fire OR deforestation OR pesticide* OR landscape). We also used the bibliographies of 24 recent papers, including a 2007 U.S. National Academy of Sciences report on the status of pollinators (NRC 2007), to search for additional studies. Our final database included 54 independent studies, 44 studies reporting abundance, and 38 studies reporting species richness, that were used in the meta-analyses (see the Supplement for the list of studies). Two of these studies were experimental and the rest were observational.

Our criteria for including a study in the meta-analysis were that the study (1) presents data on how pollinator abundance or species richness changes with anthropogenic disturbance; (2) includes replication; (3) reports the sample size; and (4) reports either the mean and standard deviation of each treatment (for categorical independent variables), or statistics such as correlation or regression coefficients (for continuous independent variables), as these are necessary to calculate effect sizes.

Authors of the original papers estimated bee abundance or richness by different means such as visitation frequency to flowers, transect surveys, pan and nesting traps, netting, etc. If a study reported multiple years of data, we used the year with the largest sample size, or if sample sizes were equal, the last year of data collection. We contacted authors for statistics on nonsignificant results, so that we could include these in the meta-analysis and avoid a bias against nonsignificant findings.

We here provide brief descriptions of the six unpublished studies used in our meta-analysis. C. Kremen (*unpublished a*), C. Kremen (*unpublished b*), and S. S. Greenleaf (*unpublished*) are described elsewhere (Greenleaf and Kremen 2006, Ricketts et al. 2008). N. M. Williams (*unpublished*) studied bee communities on farms and in oak woodland in Yolo and Solano counties, California, USA; bees were collected by hand-netting every three weeks between March and August 2002. C. Fenter and G. LeBuhn (*unpublished*) studied bee communities in 15 parks of differing area in San Francisco, California, USA; bees were collected by pan trap and hand-netting once per month from April through September 2005 within a 0.5-ha circular plots. G. LeBuhn (*unpublished*) studied oak woodland plots surrounded by varied degrees of vineyard agriculture vs. oak woodland in Napa and Sonoma Valleys, California, USA; bees were collected by pan trap and hand netting every other week from March through September in 2002 within 1-ha plots.

Grouping the data for analysis

We performed a first analysis for honey bees alone. We expected that the abundance of managed honey bees would be determined by where hives are placed rather than by human disturbance in the landscape. However, in many parts of the world honey bees exist as feral populations, and these feral bees could be affected by human disturbance. We therefore grouped the data on honey bees according to whether bees were managed or predominantly feral (unmanaged) in the researcher's study system. Sample sizes for honey bees were too small to consider further grouping variables.

We performed a second analysis for all unmanaged bees, in which we included studies of honey bees in areas where they were predominantly feral. We grouped the data on unmanaged bees according to four variables that could be important in determining outcomes: disturbance type, taxonomic category, bee sociality system, and biome. Disturbance types included the loss and/or fragmentation of habitat surrounding the study site (we were not able to distinguish habitat loss from habitat fragmentation in the studies we reviewed, and hereafter use the term "habitat loss," which is the dominant effect; Fahrig 2003), agriculture, logging, grazing, fire, pesticide use, and tillage. Bees were grouped into four taxonomic categories, which was the maximum number that was possible based on the taxonomic resolution reported in the original papers: *Bombus* (any species belonging to this genus), *Apis* (mostly *Apis mellifera*), non-*Apis* (all species that are not *Apis*, including *Bombus* in some cases where the authors did not distinguish *Bombus* as a separate category), and non-*Apis* and non-*Bombus* (any species that were neither *Apis* nor *Bombus*). *Apis* and *Bombus* are common genera reported in many studies, whereas the other 425 genera worldwide were too rarely reported to be analyzed separately. In a second classification, bees were grouped according to whether they were social or solitary, using the information provided by the authors and/or published information on the sociality of different taxa. Studies that did not separate social and solitary bees, or that included semi-social taxa, were not included in this analysis. Finally, study system biomes were categorized following Olsen et al. (2001).

Sample sizes and calculation of effect size

The studies obtained in the literature search yielded 11 data points (effect sizes) for managed honey bee abundance, 8 data points for feral honey bee abundance, 71 data points for unmanaged bee abundance, and 48 data points for unmanaged bee species richness. Most of the studies compared bee abundance or richness between less vs. more disturbed sites (categorical designs; we include multiple-level ANOVA designs here because we used the lowest and the highest levels to calculate the effect size). Thus, we used Hedge's unbiased standardized mean difference (Hedge's d) as the metric of effect size for the meta-analyses. The effect size, d, can be interpreted as the inverse-variance-weighted difference in abundance or richness of bees between natural and disturbed conditions, measured in units of standard deviations. Large differences and low variability generate the largest effect sizes (Hedges and Olkin 1985, Rosenberg et al. 2000, Gurevitch and Hedges 2001). Positive values of the effect size (d) imply positive effects of anthropogenic disturbance on bee abundance or richness whereas negative d values imply negative effects.

To calculate Hedge's d we obtained from each published paper the mean values, sample sizes, and standard deviation of bee abundance or richness in each of the two contrasting conditions (Gurevitch and Hedges 2001). For studies with continuous designs we obtained sample size along with one of the following metrics, in descending order of preference: t from multiple regression, r^2 from single regression, Pearson's r from parametric correlation, or Spearman's ρ from nonparametric correlation. We then obtained Hedge's d through arithmetical transformations using the MetaWin Calculator (Rosenberg et al. 2000).

Analyses of effect size and heterogeneity

The analyses were conducted using MetaWin version 2.0 (Rosenberg et al. 2000). Confidence intervals of effect sizes were calculated using bias-corrected bootstrap resampling procedures as described in Adams et al. (1997), except for groups with small sample sizes ($\leq$10 effect sizes), in which case bootstrap procedures were not used because they are biased due to resampling from the same small set of values (Bancroft et al. 2007). An effect of anthropogenic disturbance was considered significant if the 95% confidence intervals (CI) of the effect size (d) did not overlap zero (Rosenberg et al. 2000). Data were analyzed using random-effect models (Raudenbush 1994), which are preferable in ecological data synthesis because their assumptions are more likely to be satisfied (Gurevitch and Hedges 2001).

The heterogeneity of effect sizes was examined with Q statistics (Hedges and Olkin 1985), which can be used to determine whether the variance among effect sizes is greater than expected by chance (Cooper 1998). For the categorical comparisons (types of disturbance, biome, etc.) we examined the P values associated with Q_{bet} categories (where the subscript "bet" stands for "between"), which describe the variation in effect sizes that can be ascribed to differences between the categories.

Analyses of habitat-loss studies

Habitat loss was the most frequently studied disturbance type, accounting for 66% of our data points. We therefore did further analyses with the habitat-loss studies alone. Studies differed in the levels used for the habitat loss "treatment," in terms of either the range of variation or the extreme values encompassed. Studies including a greater range of variation, or more extreme treatment levels, might be more likely to detect significant effects. To assess the importance of the range of variation in treatment levels within a study, we divided the studies into two similar-sized groups using natural breaks in the data. This resulted in the "large range of variation" group consisting of studies in which the sites experiencing the greatest and the least habitat loss differed by ≥100 ha, ≥50% natural habitat cover in the landscape, or ≥1 km from natural habitat (depending on whether habitat patch area, percentage habitat cover surrounding the site, or distance to the nearest natural-habitat patch was used to measure habitat loss). Studies in the "small range of variation" group had less variation than this. To assess the importance of including extreme treatment levels, we compared study systems that did or did not include a site experiencing extreme habitat loss. "Extreme habitat loss" was defined as a habitat patch ≤1 ha in extent, a site surrounded by ≤5% natural-habitat cover, or a site ≥1 km from the nearest natural habitat. Systems classed as having "moderate habitat loss" did not include sites this extreme.

Publication bias

We explored the possibility of publication bias using funnel plots, which allow one to visually assess whether studies with small effect sizes are missing from the distribution of all published effect sizes. We also ran Spearman rank correlations on the same data, to examine the relationship between the standardized effect size and the sample size across studies (Begg 1994). A significant correlation would indicate a publication bias whereby larger effect sizes are more likely to be published than smaller effect sizes, when sample size is small. Finally, we used Rosenberg's 2005 fail-safe number calculator to estimate the number of nonsignificant, unpublished studies that would need to be added to a meta-analysis to nullify its overall effect size (Rosenthal 1979).

Results

Bee abundance

Anthropogenic disturbance had a significant negative effect on unmanaged bee abundance: the overall weighted-mean effect size was –0.32 (95% CI = –0.55 to –0.08; Fig. 1a). Studies of different disturbance types showed different effect sizes (Q_{bet} = 12.1, P = 0.02). In particular, studies addressing effects of habitat loss on bee abundance showed a collective negative response that differed significantly from 0, whereas other disturbance types such as logging, agriculture, and fire were not significant (Fig. 1a).

Taxonomic and ecological characteristics of unmanaged bees were less important predictors of bees' response to anthropogenic disturbance. Groups defined according to coarse taxonomic affiliation criteria did not differ significantly in their response to disturbance (Fig. 2a; Q_{bet} = 3.33, P = 0.39). However, the abundance of *Bombus* spp. (weighted-mean effect size = –0.63, 95% CI = –1.33 to –0.07) and also the abundance of species that were neither *Bombus* spp. nor *Apis* spp. (weighted-mean effect size = –0.52, 95% CI = –0.97 to –0.11) were significantly negatively affected by disturbance (Fig. 2a), while the other taxonomic groups were not. Similarly, although the difference between social and solitary bees was not significant (Q_{bet} = 2.61, P = 0.12), social bees were significantly negatively affected by disturbance (Fig. 2a; weighted-mean effect size = –0.60, 95% CI = –0.97 to –0.22), whereas solitary bees were not (Fig. 2a; weighted-mean effect size = –0.08, 95% CI = –0.65 to 0.49).

Biome type did not affect how unmanaged bees responded to disturbance (Q_{bet} = 4.07, P = 0.60). Honey bee abundance was not significantly associated with human disturbance: the weighted-mean effect size was 0.09 (95% CI = –0.16 to 0.35). Managed and feral honey bees showed similar responses to disturbance (Q_{bet} = 0.12, P = 0.69).

Bee species richness

Anthropogenic disturbance had a significant negative effect on unmanaged bee species richness: the overall weighted-mean effect size was –0.37 (95% CI = –0.68 to –0.07; Fig. 1b). In contrast to the case for abundance, bee species richness was not differentially affected by different types of disturbance (Q_{bet} = 6.4, P = 0.15). This lack of significance, however, may have been due to small sample sizes for some disturbance categories (Fig. 1b). As was the case for bee abundance, habitat loss was the only disturbance category that showed a significant effect on bee species richness (Fig. 1b; weighted-mean effect size = –0.50, 95% CI = –0.82 to –0.15).

Taxonomic and ecological characteristics of bees had less explanatory value for species richness than for abundance; again this lack of significance may have been due to our smaller sample sizes for species richness. Effect sizes on bee species richness did not differ significantly among taxonomic categories (Q_{bet} = 2.63, P = 0.55), and none of the categories showed an effect that differed significantly from zero (Fig. 2b). The difference between social and solitary bees was not quite significant (Q_{bet} = 3.29, P = 0.07), although the richness of social bees was significantly, negatively affected by disturbance (Fig. 2b; weighted-mean effect size = –0.85, 95% CI = –1.55 to –0.15) whereas the richness of solitary bees was not (Fig. 2b; weighted-mean effect size = –0.17, 95% CI = –0.744 to 0.405). The effect of disturbance on bee species richness was similar across biomes (Q_{bet} = 2.16, P = 0.63), and always nonsignificant.

Analysis of habitat-loss studies

Studies done in systems experiencing extreme habitat loss showed significant negative effects of habitat loss on

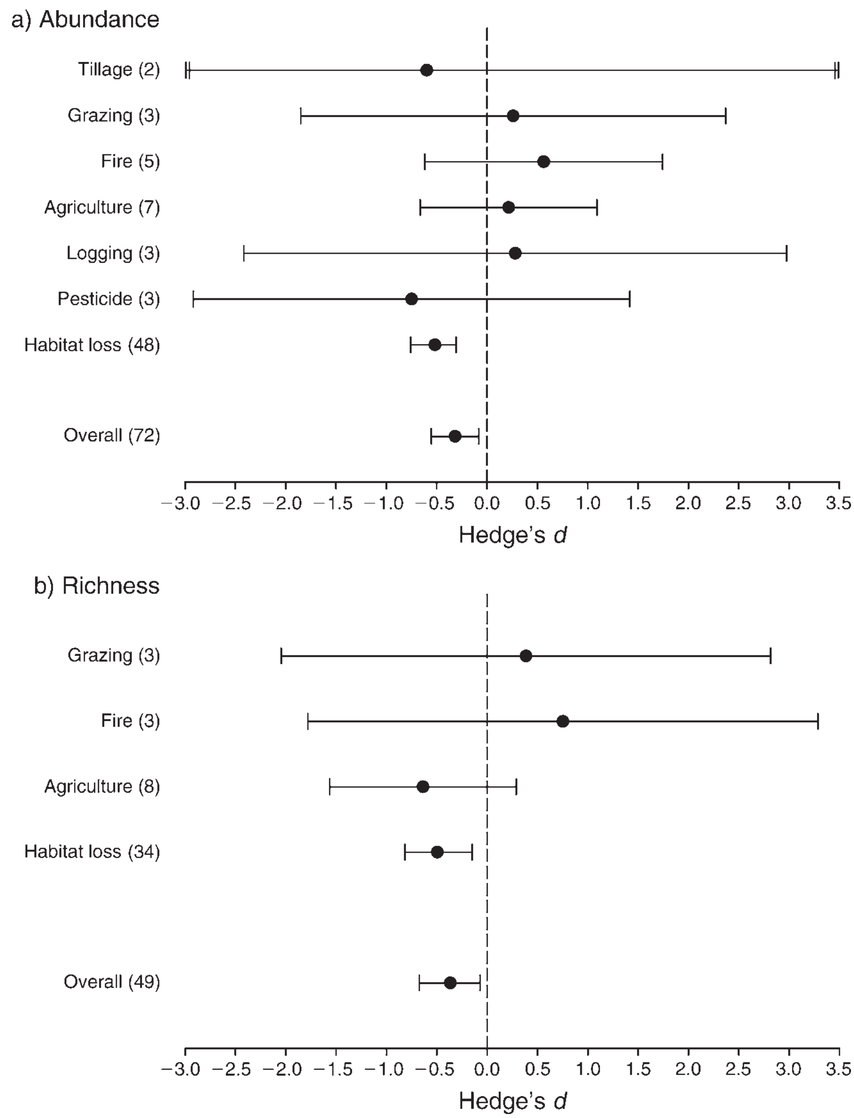

FIG. 1. Overall weighted-mean effect sizes and effect sizes of the different disturbance factors on (a) unmanaged bee abundance and (b) unmanaged bee richness. Error bars are 95% confidence intervals (CI), and effects are considered significant when a CI does not overlap 0. The CIs for tillage (truncated in the figure) are −8.49 to 7.30. Sample sizes (numbers of effect sites) are given in parentheses.

bee abundance (weighted-mean effect size = −0.67, 95% CI = −0.92 to −0.46; Fig. 3a) whereas studies done in systems experiencing only moderate habitat loss did not (weighted-mean effect size = −0.12, 95% CI = −0.52 to 0.14; Fig. 3b). This difference between the extreme and moderate systems was highly significant (Q_{bet} = 7.45, P = 0.006). Likewise for bee species richness, studies done in extreme systems showed significant negative effects (weighted-mean effect size = −0.70, 95% CI = −1.21 to −0.21; Fig. 3a) whereas the studies done in moderate systems did not (weighted-mean effect size = −0.38, 95% CI = −1.03 to 0.07; Fig. 3b). For richness, however, the difference was not significant (Q_{bet} = 0.69, P = 0.41).

In contrast, the range of variation in habitat loss treatment levels within a given study did not predict bee responses to fragmentation in terms of either abundance (for low vs. high range of variation, Q_{bet} = 0.61, P = 0.44) or species richness (Q_{bet} = 1.93, P = 0.16).

Publication bias

Visual inspection of funnel plots suggested that no publication bias exists, and statistical analysis is consistent with this conclusion (for abundance, Spearman's ρ = 0.01 and P = 0.93; for richness, ρ = −0.14 and P = 0.33). Calculation of fail-safe numbers rendered a similar result: for abundance, the fail-safe number was 513 studies, and for richness it was 272 studies. Thus, these analyses suggest that the above results on bee abundance and richness were not the result of publication bias.

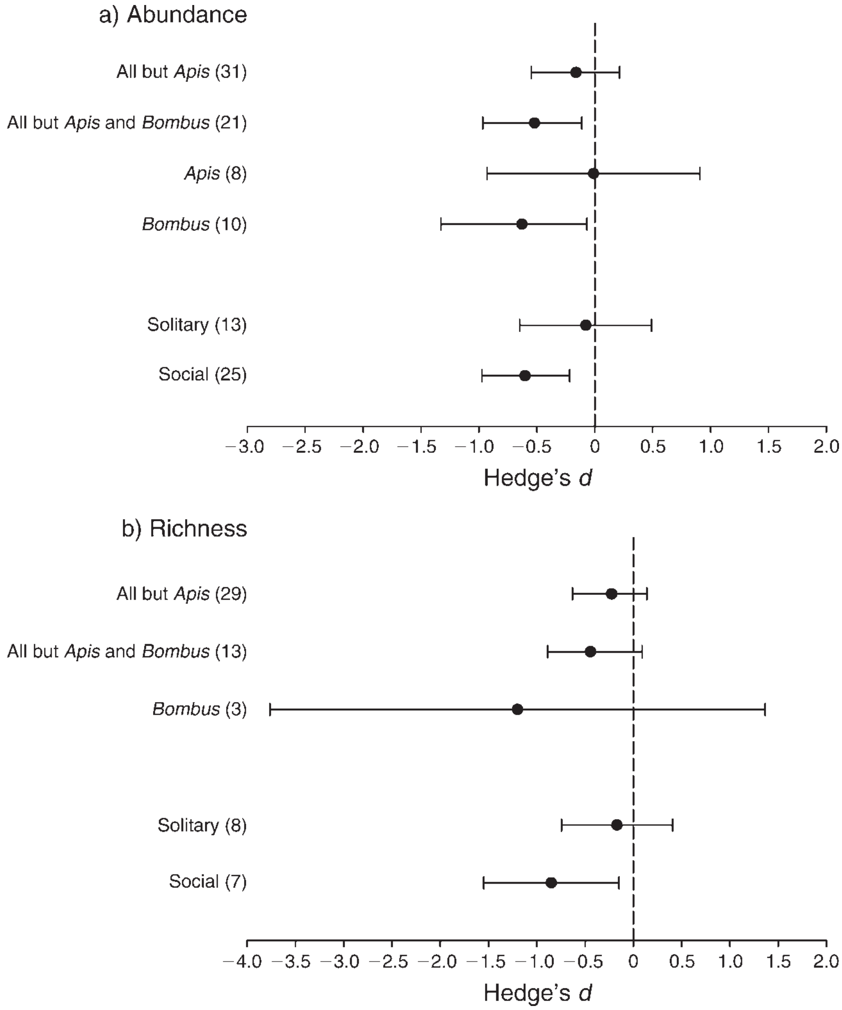

FIG. 2. Weighted-mean effect sizes as a function of bee taxon and sociality trait for (a) unmanaged bee abundance and (b) unmanaged bee species richness. Error bars are 95% confidence intervals, and effects are considered significant when CIs do not overlap zero. Sample sizes are given in parentheses.

DISCUSSION

We found a significant negative effect of human disturbance on the abundance and species richness of wild, unmanaged bees (Fig. 1). These findings represent the first quantitative review and synthesis of the literature on pollinators and human disturbance, and contribute important evidence to the debate about whether pollinators are in decline globally (Kearns et al. 1998, Ghazoul 2005*a*, *b*, Steffan-Dewenter et al. 2005, Biesmeijer et al. 2006, NRC 2007). Because pollinators are negatively affected by human land use (Fig. 1), and increasing land-use change is predicted to be the greatest cause of biodiversity losses in the future (Sala et al. 2000), future losses of pollinators seem likely. Pollinators perform a critical function in ecosystems, and their decline could affect plant communities and the pollination of crops (Kearns et al. 1998, Aizen and Feinsinger 2003, Aguilar et al. 2006, Kremen et al. 2007, Ricketts et al. 2008; but see Ghazoul 2005*a*). Many wild plant populations show pollen limitation of reproduction, i.e., increases in seed set with experimentally supplemented pollination (Ashman et al. 2004; but see Knight et al. 2006). This suggests that the population growth of many wild plant species could decrease with increasing human land use and subsequent pollinator decline.

On the other hand, the effect of disturbance on bees was not strong (weighted-mean effect size = −0.32 for abundance and −0.37 for species richness), using a rule of thumb whereby effect sizes ≤0.2 are considered "small" and those ≤0.5 are "medium" (Cohen 1969). Furthermore, bee abundance and richness were significantly reduced by habitat loss only in systems experiencing extreme habitat loss (Fig. 3). For study systems with only moderate loss, there was no significant effect on either bee abundance or species richness, although the trends are negative (Fig. 3). At present, between 50% (Vitousek et al. 1997) and 75% (Ellis and Ramankutty 2008) of the earth's land surface is converted to human use, yet 61% of the

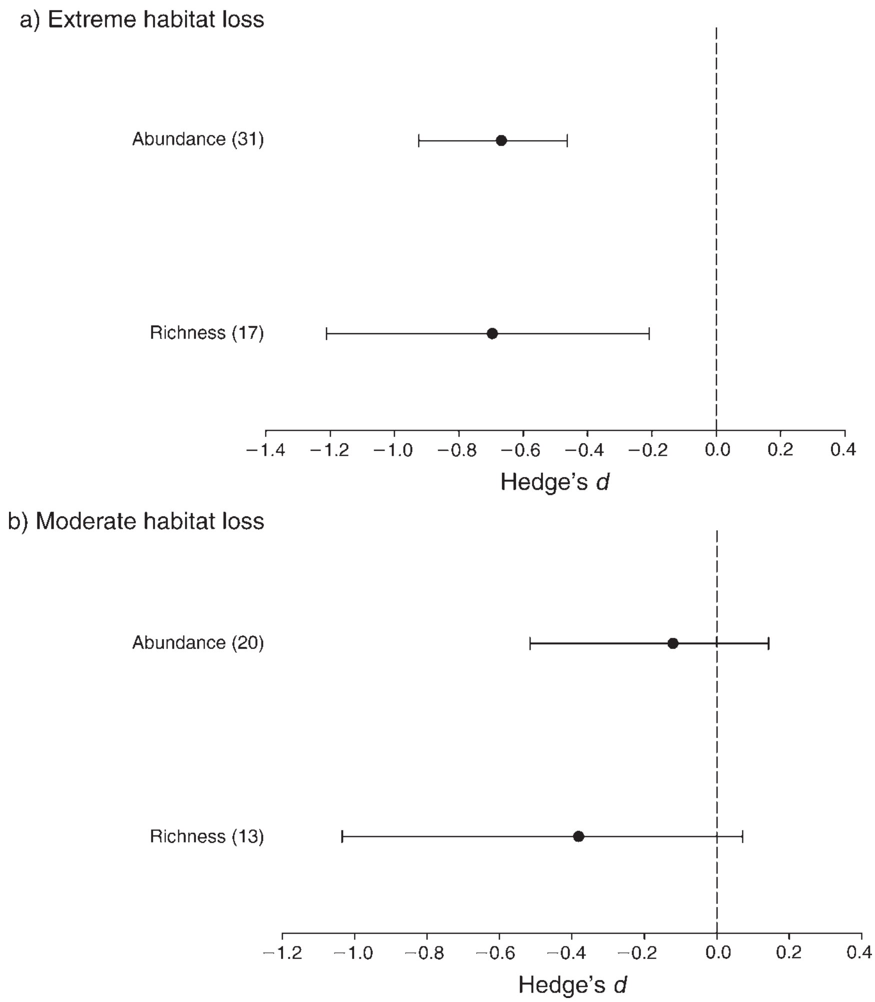

FIG. 3. Weighted-mean effect sizes for changes in bee abundance and species richness in study systems where habitat loss was (a) extreme and (b) moderate (for definitions see *Methods*). Error bars are 95% confidence intervals, and an effect is considered significant when the CI does not overlap 0. Sample sizes are given in parentheses.

studies in our meta-analyses were conducted in systems with extreme habitat loss where, for example, ≥95% of the land is converted to human use (see *Methods* for the complete definition of "extreme habitat loss"). This suggests that the studies in our meta-analysis may not be a random sample of global ecosystems. Rather, there may be a research bias whereby researchers choose to study habitat loss in systems where extreme habitat loss has occurred. If this is the case, then the appropriate scope of inference for our results is limited to ecosystems with levels of habitat loss similar to those that were studied. Expanding the scope of inference to all global ecosystems could lead to erroneously pessimistic conclusions about current global pollinator declines. To fully resolve this issue, more studies in systems with only moderate habitat loss are needed. In our review, we found only 20 studies, from a total of eight study systems, that were done in systems with moderate habitat loss.

The approach we take here provides a "snapshot" of pollinator declines across short time scales and spatial disturbance gradients. This is a proxy for long-term pollinator monitoring, which as yet has been done only in a few locations throughout the world (NRC 2007). In Western Europe, where pollinators are best monitored and where human land use is intensive, many bee species have declined over time (Mohra et al. 2004, Biesmeijer et al. 2006, NRC 2007). These findings are consistent with the results we report here.

Our meta-analyses suggest that the response of bee abundance and richness to disturbance may vary among disturbance types. Bee abundance and richness declined significantly only for one disturbance type, habitat loss. This result could reflect statistical power, given the substantially larger sample size we had for habitat loss (Fig. 1). Interestingly, however, several disturbance types showed a positive effect on bee abundance or species richness, although the uncertainty was large and sample sites small (Fig. 1). This result might indicate that, in some ecosystems, some forms of human disturbance are not detrimental to pollinators (Klemm

1996, Ghazoul 2005*a*, Winfree et al. 2007), but more studies on these disturbance types are required.

As expected, we found that the abundance of managed honey bees is not associated with anthropogenic disturbance. More interestingly, even feral honey bees were little affected by disturbance. This indicates that honey bees may be less sensitive to landscape disturbance than other bee taxa, and that they might provide a "rescue effect" for pollinator-dependent plants (Aizen and Feinsinger 1994, Dick 2001, Aguilar 2005, Chacoff and Aizen 2006, Ricketts et al. 2008). However, in our analysis this difference between honey bees and other bee taxa was not significant, possibly due to the small sample size of honey bee studies (Fig. 2a). More work on the population dynamics and function of honey bees in human-dominated ecosystems is merited (NRC 2007).

We found that social bees were more sensitive to disturbance than were solitary bees (Fig. 2). Our finding is consistent with previous work reporting the greater sensitivity of social bees to human disturbance in tropical forest systems (Klein et al. 2003, Ricketts et al. 2008) but inconsistent with other work finding solitary bees to be more sensitive to disturbance in temperate grasslands (Steffan-Dewenter et al. 2006). One possible explanation for this inconsistency is that some social, often tropical bees such as the meliponines and feral *Apis* use mature forest trees as nest sites, and should therefore be sensitive to forest loss, whereas other social, predominantly temperate-zone taxa, such as *Bombus* and some halictids, are ground-nesting and can nest in disturbed areas (Kim et al. 2006, Osborne et al. 2008). In other words, the variation in results across studies may reflect which taxa constituted the social bees in each study. In contrast to the findings for social and solitary bees, we did not find strong patterns with regard to the biome in which the study took place.

In conclusion, we found that bees are negatively affected by human disturbance. However the magnitude of this effect was not large, and it was statistically significant only in study systems where habitat loss was extreme. This work lends support to the overall view that pollinators are threatened by increasing human land use. It also stresses the large heterogeneity existing in the response of different bees to disturbance, and the fact that extrapolation of small-scale studies to the global scale should be done only with care.

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SUPPLEMENT

List of studies included in the meta-analysis, along with the calculated effect sizes (*Ecological Archives* E090-143-S1).

Hedge's d	Variance (Hedge's d)	Abundance or species richness?	Biome type	Disturbance type	Bee taxon	Bee sociality	Bee managed / unmanaged status	Reference
-1.381	0.422	Abundance	Temperate broadleaf and mixed forests	Pesticide	Bombus	Social	managed	"Plowright R.C., Pendrel B.A. & McLaren I.A. (1978). The impact of aerial fenitrothion spraying upon the population biology of bumble bees (Bombus Latr.: Hym.) in southwestern New Brunswick. Can. Entomol., 110, 1145-1156."
-1.400	0.311	Abundance	Temperate broadleaf and mixed forests	Pesticide	Bombus	Social	managed	"Plowright R.C. & Rodd F.H. (1980). The effect of aerial insecticide spraying on hymenopterous pollinators in New Brunswick. Canadian Entomologist, 112, 259-269."
-1.144	0.465	Abundance	Temperate broadleaf and mixed forests	Pesticide	Bombus	Social	managed	"Plowright R.C. & Rodd F.H. (1980). The effect of aerial insecticide spraying on hymenopterous pollinators in New Brunswick. Canadian Entomologist, 112, 259-269."
-0.082	0.400	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Apis	Social	managed	"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."
0.989	0.748	Abundance	"Mediterranean forest,woodlands and scrubland"	Agriculture	Apis	Social	managed	"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."
4.486	2.344	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Apis	Social	managed	"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."
-0.061	0.067	Abundance	"Mediterranean forest,woodlands and scrubland"	Grazing	Apis	Social	managed	"Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

0.459	0.068	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Apis	Social	managed "Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

-0.120	0.134	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Steffan-Dewenter I., M¸nzenberg U., B¸rger C., Thies C. & Tscharntke T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83, 1421-1432."

-0.216	0.134	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Heard T.A. & Exley E.M. (1994). Diversity, abundance, and distribution of insect visitors to macadamia flowers. Environmental Entomology, 23, 91-100."

0.158	0.167	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-803"

0.202	0.144	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-805"

0.154	0.087	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

-0.284	0.088	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Apis	Social	managed "Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

1.387	0.827	Abundance	Tropical and subtropical dry broadleaf forests	Fragmentation	Apis	Social	unmanaged	"Aguilar R. (2005). Effects of forest fragmentation on the reproductive success of native plant species from the Chaco Serrano forest of Central Argentina. Ph.D. thesis. National University of

Cordoba Cordoba, Argentina."

-0.617 0.698 Abundance Tropical and subtropical dry broadleaf forests Fragmentation Bombus Social unmanaged "Aguilar R. (2005). Effects of forest fragmentation on the reproductive success of native plant species from the Chaco Serrano forest of Central Argentina. Ph.D. thesis. National University of Cordoba Cordoba, Argentina."
-0.153 0.669 Abundance Tropical and subtropical dry broadleaf forests Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Aguilar R. (2005). Effects of forest fragmentation on the reproductive success of native plant species from the Chaco Serrano forest of Central Argentina. Ph.D. thesis. National University of Cordoba Cordoba, Argentina."
0.611 0.698 Abundance Temperate broadleaf and mixed forests Logging Apis Social unmanaged "Morales C.L. & Aizen M.A. (2006). Invasive mutualisms and the structure of plant-pollinator interactions in the temperate forests of north-west Patagonia, Argentina. Journal of Ecology, 94, 171-180."
0.585 0.695 Abundance Temperate broadleaf and mixed forests Logging Non-Apis and Non-Bombus All unmanaged "Morales C.L. & Aizen M.A. (2006). Invasive mutualisms and the structure of plant-pollinator interactions in the temperate forests of north-west Patagonia, Argentina. Journal of Ecology, 94, 171-180."
-1.304 0.606 Abundance Tropical and subtropical moist broadleaf forests Fragmentation Apis Social unmanaged "Chacoff N.P. & Aizen M.A. (2006). Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. Journal of Applied Ecology, 43, 18-27."
-3.689 1.351 Abundance Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis and Non-Bombus Social unmanaged "Chacoff N.P. & Aizen M.A. (2006). Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. Journal of Applied Ecology, 43, 18-27."

-0.899 0.367 Abundance Temperate broadleaf and mixed forests Fragmentation Bombus Social unmanaged "Lennartsson T. (2002). Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. Ecology, 83, 3060-3072."
-0.017 0.333 Abundance Temperate broadleaf and mixed forests Agriculture Bombus Social unmanaged "Mand M., Mand R. & Williams I.H. (2002). Bumblebees in the agricultural landscape of Estonia. Agriculture Ecosystems & Environment 89, 69-76."

-1.305 0.545 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged "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, 99, 16812-16816."
-1.440 0.347 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Bombus Social unmanaged "Greenleaf S.S. & Kremen C. (2006). Wild bee species increase tomato production but respond differently to surrounding land use in Northern California. Biological Conservation, 133, 81-87."
0.000 0.278 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Greenleaf S.S. & Kremen C. (2006). Wild bee species increase tomato production but respond differently to surrounding land use in Northern California. Biological Conservation, 133, 81-87."
-0.189 0.118 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged Greenleaf S.S. (Unpublished). Bee life history mediates response to farm management and loss of natural habitat in a mixed wild and agricultural landscape.
-1.177 0.138 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Social unmanaged Greenleaf S.S. (Unpublished). Bee life history mediates response to farm management and loss of natural habitat in a mixed wild and agricultural landscape.
-1.307 1.214 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged "Kim J., Williams N.M. & Kremen C. (2006). Effect 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."
-0.880 0.402 Abundance Temperate broadleaf and mixed forests Agriculture Bombus Social unmanaged "Sepp K., Mikk 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."
0.144 0.182 Abundance "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged LeBuhn G. (Unpublished). Data from Napa and Sonoma counties.
-0.959 0.149 Abundance Temperate coniferous forest Fragmentation Bombus Social unmanaged "Hatfield R. & LeBuhn G. (2007). Patch and landscape factors shape community assemblage of bumble bees, Bombus spp. (Hymenoptera: Apidae), in montane meadows. Biological Conservation 139, 150-158."

1.824 0.405 Abundance "Mediterranean forest,woodlands and scrubland" Fire Non-Apis and Non-Bombus Solitary unmanaged "Potts S.G., Vulliamy B., Dafni A., O'Toole C., Roberts S. & Willmer P. (2003). Response of plant-pollinator communities following fire: changes in diversity, abundance and reward structure. Oikos, 101, 103-112."

-1.532	0.517	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Bombus	Social	unmanaged	"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."

-0.475	0.411	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Non-Apis and Non-Bombus	Solitary	unmanaged	"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."

0.405	0.680	Abundance	"Mediterranean forest,woodlands and scrubland"	Agriculture	Non-Apis	All	unmanaged	"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."

1.955	0.985	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Non-Apis	All	unmanaged	"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."

0.869	0.073	Abundance	"Mediterranean forest,woodlands and scrubland"	Grazing	Non-Apis	All	unmanaged	"Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

1.065	0.076	Abundance	"Mediterranean forest,woodlands and scrubland"	Fire	Non-Apis	All	unmanaged	"Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

-0.660	0.527	Abundance	Tropical and subtropical moist broadleaf forests	Fragmentation	Apis	Social	unmanaged	"Ricketts T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology, 18, 1262-1271."

-2.440	0.872	Abundance	Tropical and subtropical moist broadleaf forests	Fragmentation	Non-Apis	All	unmanaged	"Ricketts T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology, 18,

1262–1271."

0.023 0.160 Abundance Temperate broadleaf and mixed forests Pesticide Bombus Social unmanaged "Shuler R.E., Roulston T., & Farris, G. E. (2005). Farming practices influence wild pollinator populations on squash and pumpkin. Journal of Economic Entomology, 98, 790–795."

-0.039 0.250 Abundance Temperate broadleaf and mixed forests Tillage Bombus Social unmanaged "Shuler R.E., Roulston T., & Farris, G. E. (2005). Farming practices influence wild pollinator populations on squash and pumpkin. Journal of Economic Entomology, 98, 790–795."

-0.213 0.161 Abundance Temperate broadleaf and mixed forests Pesticide Non-Apis and Non-Bombus Solitary unmanaged "Shuler R.E., Roulston T., & Farris, G. E. (2005). Farming practices influence wild pollinator populations on squash and pumpkin. Journal of Economic Entomology, 98, 790–795."

-1.177 0.278 Abundance Temperate broadleaf and mixed forests Tillage Non-Apis and Non-Bombus Solitary unmanaged "Shuler R.E., Roulston T., & Farris, G. E. (2005). Farming practices influence wild pollinator populations on squash and pumpkin. Journal of Economic Entomology, 98, 790–795."

-0.137 0.084 Abundance Tropical and subtropical moist broadleaf forests Fragmentation Non-Bombus All unmanaged "Klein A.M., Steffan-Dewenter I. & Tscharntke T. (2003a). Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society of London Series B Biological Sciences, 270, 955–961."

0.633 0.140 Abundance Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis All unmanaged "Klein A.M., Steffan-Dewenter I. & Tscharntke T. (2003b). Pollination of Coffea canephora in relation to local and regional agroforestry management. Journal of Applied Ecology, 40, 837–845."

-0.798 0.054 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. & Tscharntke T. (1999). Effects of habitat isolation on pollinator communities and seed set. Oecologia, 121, 432–440."

-1.137 0.155 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I., M¸nzenberg U. & Tscharntke T. (2001). Pollination, seed set and seed predation on a landscape scale. Proceedings of the Royal

Society of London Series B, 268, 1685–1690."

-2.240 0.217 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I., M¸nzenberg U., B¸rger C., Thies C. & Tscharntke T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83, 1421–1432."

0.500 0.138 Abundance Temperate broadleaf and mixed forests Grazing Non-Apis All unmanaged "Steffan-Dewenter I. & Leschke K. (2003). Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. Biodiversity and Conservation, 12, 1953–1968."

-0.452 0.046 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology, 17, 1036–1044."

-0.642 0.047 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology, 17, 1036–1044."

-0.343 0.135 Abundance Temperate broadleaf and mixed forests Fragmentation Bombus Social unmanaged "Westphal C., Steffan-Dewenter I. & Tscharntke T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters, 6, 961–965."

1.775 0.279 Abundance Tropical and subtropical moist broadleaf forests Agriculture Non-Apis Solitary unmanaged "Klein A.-M., Steffan-Dewenter I., Buchori D. & Tscharntke 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."

-1.713 0.273 Abundance Tropical and subtropical moist broadleaf forests Agriculture Non-Apis Social unmanaged "Klein A.-M., Steffan-Dewenter I., Buchori D. & Tscharntke 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."

-0.786 0.090 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "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. Waser N & Ollerton J). University of Chicago Press Chicago, pp. 387-407."

0.514 0.517 Abundance Tropical and subtropical dry broadleaf forests Fragmentation Apis Social unmanaged "Aizen M.A. & Feinsinger P. (1994). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine ""chaco serrano"". Ecological Applications, 4, 378-392."

0.517 0.517 Abundance Tropical and subtropical dry broadleaf forests Fragmentation Apis Social unmanaged "Aizen M.A. & Feinsinger P. (1994). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine ""chaco serrano"". Ecological Applications, 4, 378-392."

-0.913 0.552 Abundance Tropical and subtropical dry broadleaf forests Fragmentation Non-Apis All unmanaged "Aizen M.A. & Feinsinger P. (1994). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine ""chaco serrano"". Ecological Applications, 4, 378-392."

-1.327 0.610 Abundance Temperate broadleaf and mixed forests Grazing all All unmanaged "V·zquez D.P. & Simberloff D. (2003). Changes in interaction biodiversity induced by an introduced ungulate. Ecology Letters, 6, 1077-1083."

2.855 0.486 Abundance Temperate broadleaf and mixed forests Agriculture Non-Apis All unmanaged "Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21, 213-223."

1.338 0.257 Abundance Temperate broadleaf and mixed forests Urbanization Non-Apis All unmanaged "Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21, 213-223."

0.950 0.079 Abundance Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21, 213-223."

1.171 1.171 Abundance Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis and Non-Bombus Social unmanaged "Eltz T., Bruhl C.A., van der Kaars S. & Linsenmair K.E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia, 131,

27–34."

-0.313	0.616	Abundance	Tropical and subtropical moist broadleaf forests	Logging	Non-Apis and Non-Bombus	Social	unmanaged	"Eltz T., Bruhl C.A., van der Kaars S. & Linsenmair K.E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia, 131, 27–34."

-2.797	0.539	Abundance	Temperate broadleaf and mixed forests	Pesticide	Non-Apis	All	unmanaged	"Kevan P.G. (1975). Forest application of the insecticide Fenitrothion and its effects on wild bee pollinators of low-bush blueberries (Vaccinium spp.) in southern New Brunswick, Canada. Biological Conservation, 7, 301–309."

-1.713	0.182	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis and Non-Bombus	Social	unmanaged	"Heard T.A. & Exley E.M. (1994). Diversity, abundance, and distribution of insect visitors to macadamia flowers. Environmental Entomology, 23, 91–100."

-2.016	0.603	Abundance	"Tropical and subtropical grasslands, savannahs, and shrublands"	Fragmentation	Apis	Social	unmanaged	"Blanche K.R., Ludwig J.A. & Cunningham S.A. (2006). Proximity to rainforest enhances pollination and fruit set in macadamia and longan orchards in north Queensland, Australia. Journal of Applied Ecology, 43, 1182–1187."

0.871	0.365	Abundance	"Tropical and subtropical grasslands, savannahs, and shrublands"	Fragmentation	Apis	Social	unmanaged	"Blanche K.R., Ludwig J.A. & Cunningham S.A. (2006). Proximity to rainforest enhances pollination and fruit set in macadamia and longan orchards in north Queensland, Australia. Journal of Applied Ecology, 43, 1182–1187."

-0.321	0.338	Abundance	"Tropical and subtropical grasslands, savannahs, and shrublands"	Fragmentation	Non-Apis and Non-Bombus	Solitary	unmanaged	"Blanche K.R., Ludwig J.A. & Cunningham S.A. (2006). Proximity to rainforest enhances pollination and fruit set in macadamia and longan orchards in north Queensland, Australia. Journal of Applied Ecology, 43, 1182–1187."

-0.505	0.344	Abundance	"Tropical and subtropical grasslands, savannahs, and shrublands"	Fragmentation	Non-Apis and Non-Bombus	Social	unmanaged	"Blanche K.R., Ludwig J.A. & Cunningham S.A. (2006). Proximity to rainforest enhances pollination and fruit set in macadamia and longan orchards in north Queensland, Australia. Journal of Applied Ecology, 43, 1182–1187."

-0.565	0.407	Abundance	"Mediterranean forest,woodlands and scrubland"	Agriculture	Non-Apis All
unmanaged	"Williams N.M. (Unpublished). Data from Yolo County, 2002."

-0.544	0.207	Abundance	"Mediterranean forest,woodlands and scrubland"	Fragmentation	Non-Apis All	unmanaged
Kremen C. (Unpublished-a). Unpublished data on almond.

0.360	0.203	Abundance	"Mediterranean forest,woodlands and scrubland"	Fragmentation	Non-Apis and Non-Bombus	Solitary
unmanaged	Kremen C. (Unpublished-b). Unpublished data on muskmelon.

-0.201	0.168	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-802"

-0.848	0.156	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-804"

-0.397	0.093	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-806"

0.037	0.118	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-807"

0.353	0.156	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-808"

-0.201	0.155	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis	All	unmanaged	"Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-809"

0.101	0.087	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis	All	unmanaged	"Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

0.070	0.087	Abundance	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis	All	unmanaged	"Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

-1.368	0.112	Abundance	Boreal forests / taiga	Fragmentation	Non-Apis	All	unmanaged	"Morandin L.A. & Winston M.L. (2006). Pollinators provide economic incentive to preserve natural land in agroecosystems. Agriculture, Ecosystems & Environment, 116, 289-292."

-1.828	1.418	Abundance	Tropical and subtropical moist broadleaf forests	Fragmentation	Non-Apis and Non-Bombus	Solitary	unmanaged	"Becker P., Moure J.S. & Peralta F.J.A. (1991). More about euglossine bees in Amazonian forest fragments. Biotropica, 23, 586-591."

-4.249	1.629	Abundance	Tropical and subtropical moist broadleaf forests	Fragmentation	Non-Apis and Non-Bombus	Solitary	unmanaged	"Powell A.H. & Powell G.V.N. (1987). Population dynamics of male euglossine bees in Amazonian forest fragments. Biotropica, 19, 176-179."

-0.656	0.703	Species richness	Tropical and subtropical dry broadleaf forests	Fragmentation	Non-Apis	All	unmanaged	"Aguilar R. (2005). Effects of forest fragmentation on the reproductive success of native plant species from the Chaco Serrano forest of Central Argentina. Ph.D. thesis. National University of Cordoba Cordoba, Argentina."

-0.062	0.191	Species richness	"Mediterranean forest,woodlands and scrubland"	Fragmentation	All bees	All	unmanaged	"Dupont Y.L. & Nielsen B.O. (2006). Species composition, feeding specificity and larval trophic level of flower-visiting insects in fragmented versus continuous heathlands in Denmark. Biological Conservation, 131, 475-485."

-3.325 1.588 Species richness "Mediterranean forest,woodlands and scrubland" Agriculture All bees All unmanaged "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 Journal of Applied Ecology, 44, 41-49."

-0.942 0.370 Species richness Temperate broadleaf and mixed forests Agriculture Bombus Social unmanaged "Mand M., Mand R. & Williams I.H. (2002). Bumblebees in the agricultural landscape of Estonia. Agriculture Ecosystems & Environment 89, 69-76."

-1.769 0.624 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged "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, 99, 16812-16816."

-1.177 0.138 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged Greenleaf S.S. (Unpublished). Bee life history mediates response to farm management and loss of natural habitat in a mixed wild and agricultural landscape.

-1.747 0.553 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged "Kim J., Williams N.M. & Kremen C. (2006). Effect 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."

-2.005 0.549 Species richness Temperate broadleaf and mixed forests Agriculture Bombus Social unmanaged "Sepp K., Mikk 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."

-0.729 0.194 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged LeBuhn G. (Unpublished). Data from Napa and Sonoma counties.

-0.853 0.145 Species richness Temperate coniferous forest Fragmentation Bombus Social unmanaged "Hatfield R. & LeBuhn G. (2007). Patch and landscape factors shape community assemblage of bumble bees, Bombus spp. (Hymenoptera: Apidae), in montane meadows. Biological Conservation 139, 150-158."

-1.155 0.156 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Fenter C. & LeBuhn G. (Unpublished). Bees (Apoidea: Hymenoptera) are persisting in San Francisco parks, owing to habitat quality and the surrounding matrix."

-0.811 0.207 Species richness Deserts and xeric shrublands Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Cane J.H., Minckley R., Kervin L., Roulston T. & Williams N. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Applications, 632-644."

1.106 0.329 Species richness "Mediterranean forest,woodlands and scrubland" Fire Non-Apis and Non-Bombus Solitary unmanaged "Potts S.G., Vulliamy B., Dafni A., O'Toole C., Roberts S. & Willmer P. (2003). Response of plant-pollinator communities following fire: changes in diversity, abundance and reward structure. Oikos, 101, 103-112."

0.716 0.709 Species richness "Mediterranean forest,woodlands and scrubland" Agriculture Non-Apis All unmanaged "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."

0.226 0.671 Species richness "Mediterranean forest,woodlands and scrubland" Fire Non-Apis All unmanaged "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."

0.785 0.072 Species richness "Mediterranean forest,woodlands and scrubland" Fire Non-Apis All unmanaged "Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

0.199 0.067 Species richness "Mediterranean forest,woodlands and scrubland" Grazing Non-Apis All unmanaged "Vulliamy B., Simon G. Potts and P. G. Willmer (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos, 114, 529-543."

-6.748 3.346 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis All unmanaged

"Ricketts T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conservation Biology, 18, 1262-1271."

-1.335 0.102 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Bombus All unmanaged "Klein A.M., Steffan-Dewenter I. & Tscharntke T. (2003a). Fruit set of highland coffee increases with the diversity of pollinating bees. Proceedings of the Royal Society of London Series B Biological Sciences, 270, 955-961."

-0.747 0.143 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis All unmanaged "Klein A.M., Steffan-Dewenter I. & Tscharntke T. (2003b). Pollination of Coffea canephora in relation to local and regional agroforestry management. Journal of Applied Ecology, 40, 837-845."

-0.864 0.055 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. & Tscharntke T. (1999). Effects of habitat isolation on pollinator communities and seed set. Oecologia, 121, 432-440."

-1.905 0.194 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I., M¸nzenberg U., B¸rger C., Thies C. & Tscharntke T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83, 1421-1432."

-0.026 0.133 Species richness Temperate broadleaf and mixed forests Grazing Non-Apis All unmanaged "Steffan-Dewenter I. & Leschke K. (2003). Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. Biodiversity and Conservation, 12, 1953-1968."

-0.343 0.045 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology, 17, 1036-1044."

0.436 0.046 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conservation Biology, 17, 1036-1044."

-0.651 0.140 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Steffan-Dewenter I. (2002). Landscape context affects trap-nesting bees, wasps, and their natural enemies. Ecological Entomology, 27, 631-637."

-1.260 0.240 Species richness Tropical and subtropical moist broadleaf forests Agriculture Non-Apis Social unmanaged "Klein A.-M., Steffan-Dewenter I., Buchori D. & Tscharntke 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."

0.222 0.201 Species richness Tropical and subtropical moist broadleaf forests Agriculture Non-Apis Solitary unmanaged "Klein A.-M., Steffan-Dewenter I., Buchori D. & Tscharntke 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."

-2.989 0.176 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "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. Waser N & Ollerton J). University of Chicago Press Chicago, pp. 387-407."

-0.635 0.525 Species richness Tropical and subtropical dry broadleaf forests Fragmentation Non-Apis All unmanaged "Aizen M.A. & Feinsinger P. (1994). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine ""chaco serrano"". Ecological Applications, 4, 378-392."

-0.333 0.107 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis Social unmanaged "Brown J.C. & Albrecht C. (2001). The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. Journal of Biogeography, 28, 623-634."

1.339 0.612 Species richness Temperate broadleaf and mixed forests Grazing All bees All unmanaged "V·zquez D.P. & Simberloff D. (2003). Changes in interaction biodiversity induced by an introduced ungulate. Ecology Letters, 6, 1077-1083."

2.146 0.393 Species richness Temperate broadleaf and mixed forests Agriculture Non-Apis All unmanaged "Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21,

213–223."

0.670	0.225	Species richness	Temperate broadleaf and mixed forests	Urbanization	Non-Apis	All	unmanaged	"Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21, 213–223."

1.236	0.085	Species richness	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis	All	unmanaged	"Winfree R., Griswold T. & Kremen C. (2007a). Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, 21, 213–223."

0.723	1.065	Species richness	Tropical and subtropical moist broadleaf forests		Fragmentation	Non-Apis and Non-Bombus	Social	unmanaged	"Eltz T., Bruhl C.A., van der Kaars S. & Linsenmair K.E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia, 131, 27–34."

–1.045	0.661	Species richness	Tropical and subtropical moist broadleaf forests		Logging	Non-Apis and Non-Bombus	Social	unmanaged	"Eltz T., Bruhl C.A., van der Kaars S. & Linsenmair K.E. (2002). Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia, 131, 27–34."

1.301	0.162	Species richness	Temperate broadleaf and mixed forests	Fragmentation	Non-Apis	All	unmanaged	"Dauber J., Hirsch M., Simmering D., Waldhardt R., Otte A. & Wolters V. (2003). Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture Ecosystems & Environment, 98, 321–329."

0.584	0.348	Species richness	"Tropical and subtropical grasslands, savannahs, and shrublands"	Fragmentation	Non-Apis	All	unmanaged	"Blanche K.R., Ludwig J.A. & Cunningham S.A. (2006). Proximity to rainforest enhances pollination and fruit set in macadamia and longan orchards in north Queensland, Australia. Journal of Applied Ecology, 43, 1182–1187."

–2.252	0.623	Species richness	"Mediterranean forest,woodlands and scrubland"	Agriculture	Non-Apis	All	unmanaged	"Williams N.M. (Unpublished). Data from Yolo County, 2002."

–1.841	0.285	Species richness	"Mediterranean forest,woodlands and scrubland"	Fragmentation	Non-Apis	All	unmanaged	Kremen C. (Unpublished-a). Unpublished data on almond.

0.480 0.206 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus Solitary unmanaged Kremen C. (Unpublished-b). Unpublished data on muskmelon.

-0.129 0.154 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-810"

0.471 0.158 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Winfree R., Williams N.M., Gaines H., Ascher J.S. & Kremen C. (2008). Wild pollinators provide the majority of crop visitation across land use gradients in New Jersey and Pennsylvania. Journal of Applied Ecology, 46, 793-811"

0.020 0.087 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

0.272 0.088 Species richness Temperate broadleaf and mixed forests Fragmentation Non-Apis All unmanaged "Winfree R., Williams N.M., Dushoff J. & Kremen C. (2007b). Native bees provide insurance against ongoing honey bee losses. Ecology Letters, 10, 1105-1113."

1.146 1.164 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Becker P., Moure J.S. & Peralta F.J.A. (1991). More about euglossine bees in Amazonian forest fragments. Biotropica, 23, 586-591."

0.248 0.403 Species richness "Mediterranean forest,woodlands and scrubland" Fragmentation Non-Apis and Non-Bombus All unmanaged "Donaldson J., N‰nni I., Zachariades C. & Kemper J. (2002). Effects of habitat fragmentation on pollinator diversity and plant reproductive success in Renosterveld Shrublands of South Africa. Conservation Biology, 16, 1267-1276."

-0.275 0.084 Species richness Tropical and subtropical moist broadleaf forests Fragmentation Non-Apis and Non-Bombus Solitary unmanaged "Klein A., Steffan-Dewenter I. & Tscharntke T. (2006). Rain forest promotes trophic interactions and diversity of

trap-nesting Hymenoptera in adjacent agroforestry. Journal of Animal Ecology, 75, 315–323."