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Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes

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Summary

1. Bees are a functionally important and economically valuable group, but are threatened by land-use conversion and intensification. Such pressures are not expected to affect all species identically; rather, they are likely to be mediated by the species' ecological traits.

2. Understanding which types of species are most vulnerable under which land uses is an important step towards effective conservation planning.

3. We collated occurrence and abundance data for 257 bee species at 1,584 European sites from surveys reported in 30 published papers (70,056 records), and combined them with species-level ecological trait data. We used mixed-effects models to assess the importance of land use (land-use class, agricultural use-intensity and a remotely-sensed measure of vegetation), traits, and trait × land use interactions, in explaining species occurrence and abundance.

4. Species' sensitivity to land use was most strongly influenced by foraging range and flight season, but also by niche breadth, phenology and reproductive strategy, with effects that differed among cropland, pastoral and urban habitats.

5. *Synthesis and applications.* Rather than targeting particular species or settings, conservation actions may be more effective if focused on mitigating situations where species' traits strongly and negatively interact with land-use pressures. We find evidence that low-intensity agriculture can maintain relatively diverse bee communities; in more intensive settings, added floral resources may be beneficial, but will require careful placement with respect to foraging ranges of smaller bee species. Protection of semi-natural habitats is essential, however; in particular, conversion to urban environments could have severe effects on bee diversity and pollination services. Our results highlight the importance of exploring how ecological traits mediate species responses to human impacts, but further research is needed to enhance the predictive ability of such analyses.

Keywords

Life-history traits; human impacts; ecosystem services; biodiversity, pollinators, land-use change, land-use intensification.

Introduction

Bees are key providers of pollination services, which are vital for food security and the persistence of many wild plants (Klein *et al.* 2007; Ollerton, Winfree & Tarrant 2011). However, many bee species are threatened by changing and intensifying land use (Ollerton *et al.* 2014; Potts *et al.* 2010).

Land-use change, such as conversion from semi-natural habitats to human-dominated land-uses, can greatly impact bee communities. Urbanization, agricultural expansion and abandonment are ongoing drivers of land-use change in Europe (Verburg *et al.* 2006), which can affect bee diversity through reduced floral and nesting resources (Forrest *et al.* 2015; Hernandez, Frankie & Thorp 2009). Semi-natural habitats are prime targets for land conversion (Verburg *et al.* 2006). Such habitat loss can affect pollination of crops as well as of wild flowers: as central place foragers, bees often forage up to a few kilometres away from their nests (Greenleaf *et al.* 2007) so semi-natural habitat can provide spill-over of pollination services to nearby cropland and vice-versa (Blitzer *et al.* 2012).

Agricultural intensification—through decreased crop diversity and increased external inputs—is another major pressure, which can impact bees directly by increasing mortality and indirectly by decreasing resource availability (Potts *et al.* 2010; Roulston & Goodell 2011). For instance, neonicotinoid pesticides restrict colony growth and queen production in bumblebees, and limit foraging success and survival of honeybees (Henry *et al.* 2012; Whitehorn *et al.* 2012). Nitrogen fertilizer and herbicides can affect bees indirectly by reducing the diversity of plants (Kleijn *et al.* 2009) and thus foraging resources (Roulston & Goodell 2011). Reductions in non-crop habitat as management intensifies can reduce the availability of nesting sites, while increased tillage in cropland disturbs the nesting sites of some species (Shuler, Roulston & Farris 2005).

These pressures are unlikely to affect all species identically, but are expected to be mediated by species' traits (Murray *et al.* 2009; Roulston & Goodell 2011). In general, species with narrower niches—in terms of space, time, phenotype, or interspecific interactions—are predicted to be more sensitive than generalists (Den Boer 1968; Kassen 2002). Bee species' traits may specifically influence vulnerability to land use; for instance, larger foraging ranges facilitate foraging in fragmented landscapes, but may increase the likelihood of contact with pesticides and indicate greater resource needs. Others traits can influence susceptibility to demographic stress and stochastic events; for example, a higher reproductive capacity may buffer species against disturbances, but may indicate greater resource requirements.

Identifying traits that render species vulnerable to human impacts can help inform and guide effective conservation priorities. Most previous attempts to identify ecological correlates of bee vulnerability to human impacts have focused on a relatively small number of sites and threats, or on museum collections rather than ecological survey data (e.g. Bartomeus *et al.* 2013a; Vázquez & Simberloff 2002). One exception is Williams *et al*'s (2010) global multi-species analysis, which found that some traits correlated with vulnerability to multiple threats: for instance, above- versus below-ground nesting influenced species' susceptibility to fire, isolation and agricultural management practices. Vulnerability traits can also be threat-specific (Owens & Bennett 2000; Purvis *et al.* 2005), in which case conservation actions would need to focus on populations experiencing 'dangerous' combinations of local pressures and ecological traits. For instance, social species may be more sensitive in intensively-used cropland— where enhanced foraging capacity can increase exposure to pesticides and thus affect mortality and colony success—but relatively less sensitive in urban areas, where greater foraging capacities may enable persistence (Banaszak-Cibicka & Żmihorski 2011).

In the broadest analysis of European bees to date, we explore whether ecological traits influence the responses of 257 bee species to local land-use pressures at 1,584 European sites. Unlike the study by Williams *et al* (2010), we analyse multiple traits within the same models. We aim to identify the traits and land-use pressures associated with a species having low probability of occurrence and low abundance; we also aim to estimate the relative importance of land use, traits and the interaction between them in shaping species' occurrence and abundance. We hypothesize that resource and phenological niche breadth, foraging range and reproductive strategy will all influence species' sensitivity to land use.

Materials and methods

Data collation

Data were sought from published comparisons where bee abundance and occurrence were sampled in multiple sites within agricultural landscapes. Papers based on potentially suitable data were identified by systematically searching Web of Science during 2011-2012 (Table S1.1, Supporting Information), searching journal alerts and assessing references cited in reviews. Criteria for selection were (i) multiple European sites were sampled for bee abundance or occurrence using the same sampling method within the same season; (ii) at least one site was <1km from agricultural land; (iii) geographic coordinates were available for each site; and, (iv) sites were sampled since February 2000, so that diversity data could be matched with remote-sensed data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). MODIS data were chosen over other remote-sensed imagery as they are available at high spatial (250m) and temporal (16 day) resolutions and are easily integrated into R analyses (Tuck *et al.* 2014).

We extracted site-level occurrence and abundance data from suitable papers where possible. Raw data were usually not included within the paper or supplementary files so we asked corresponding authors for these data. Relevant data were available from 30 papers, hereafter referred to as sources (Table S1.2). Some sources report separately data collected in different ways or seasons. We term each separate data set a 'study': within, but not between, studies, diversity data can be compared straightforwardly among sites because sampling protocols were the same. We also split datasets that spanned multiple countries into separate studies for each country to account for biogeographic variation in diversity. Differences in sampling effort within a study were corrected for, assuming that recorded abundance increases linearly with sampling effort. Within each study, we recorded any blocked or split-plot design. In all but one case, this was the sampling design of an observational study. Only one study included was an experimental project, where only the control data were extracted; this study had extremely low influence on the final models (based on Cook's distance, influence.ME package, Niewenhuis, te Grotenhuis & Pelzer 2012) and did not qualitatively change the results.

The major land use and use intensity at each site was assessed based on information in the associated paper, using the scheme described in Hudson *et al.* (2014, reproduced in Table S1.3).

Land use was classified as secondary vegetation, cropland, pasture or urban. The use-intensity scale—a qualitative measure of the extent of human disturbance—is coarse (three levels: minimal, light and intense), but can be applied in a wide range of settings (Hudson *et al.* 2014). Many combinations of land use and use intensity had too few sites to permit robust modeling. The data were therefore coarsened into a single factor (hereafter, Land Use and Intensity, LUI), collapsing levels to ensure adequate sample sizes. The final dataset had the following LUI classes: secondary vegetation (165 sites); minimally-used cropland (168); lightly-used cropland (415); intensively-used cropland (653); pasture (138); and urban (45).

As well as using a coarse, discrete representation of land use, we also used remotely-sensed mean Normalized Difference Vegetation Index (NDVI), to capture additional variation in vegetation between sites. NDVI is highly correlated with above-ground biomass and net primary productivity (Pettorelli *et al.* 2005), and often correlates positively with plant and invertebrate species richness even at relatively small spatial scales (e.g. Gould 2000; Lassau & Hochuli 2008). For each site, we dowloaded MODIS MOD13Q1 (collection 5) NDVI data (composited for 16 days) at 250m spatial resolution for up to three years, with the final year being the year of sampling. Poor-quality observations were removed and linear interpolation applied to remaining data. The time series was averaged to give mean NDVI (henceforth, mNDVI). NDVI data were downloaded and processed using the MODISTools package (Tuck *et al.* 2014). In our dataset, high mNDVI is unlikely to be driven by densely forested areas (which may not benefit bees in temperate systems, Winfree *et al.* 2007): wooded sites were only present in two of 24 sources (three sites in woodland and two in mixed woodland/agriculture) and these sources were not particularly influential in the final models (as judged by Cook's distance values; all <= 0.097).

Data on species traits were compiled by SR and MK; morphometric data came from museum specimens and other traits from many published and unpublished sources (Table S2.1). We used traits reflecting resource specialization, phenology, reproductive strategy and foraging range. Flight season duration and intertegular distance were treated as continuous variables, and all other traits as factors. Sample sizes were increased by collapsing factor levels where necessary to permit robust modelling (Table 1 and Table S2.1).

[Table 1 about here.]

Analysis

We excluded 14 sites for which LUI or mNDVI were not available, and 12 species for which not all trait values were known.

The diversity data were zero-inflated with a positive mean–variance relationship, but were not exclusively counts, because abundance measurements included densities, so a discrete error distribution (e.g. Poisson) could not be used. Instead, the analysis was carried out in two stages, equivalent to a hurdle model, using mixed-effects models (lme4 package version 1.1-6, Bates, Maechler & Bolker 2013). Species presence (and detection) was modelled using a binomial error structure; then the (log-transformed) abundance of present species was modelled using normal errors (Newbold *et al.* 2014). Model assumptions were checked and found to be reasonable (e.g. Fig. S3.1).

We used mixed effects models to account for non-independence of data due to differences in collectors (source), sampling methodologies and biogeography (study), the spatial structure of sites (block), and taxonomy (family and species). The initial, maximal random-effects structure was block (nested within study within source), crossed with species (nested within family). We also tested an alternative structure of block nested within study within sampling method, but this performed less well (results not shown), so was not pursued. More complicated random effect structures (e.g. random slopes) could not be fitted due to computational limitations. Both the presence and abundance models had the same initial maximal fixed-effects model structure, containing all land use (LUI and mNDVI) and trait variables, as well as all two-way interactions between land use and traits. We determined the best random-effect structures using likelihood ratio tests (Zuur *et al.* 2009), comparing all formulations.

Full models were assessed for multicollinearity using generalized variance inflation factors (GVIFs, Zuur *et al.* 2009), which never breached the threshold of 10 (Table S3.1 and S3.2). We used backwards stepwise model simplification based on likelihood ratio tests to reduce model complexity as far as possible and to determine whether interactive effects between traits and land use were retained in the final model (Zuur *et al.* 2009). Model simplification reduced the GVIFs

(Table S3.3). We assessed robustness of parameter estimates by bootstrapping data points, using 1,000 iterations for the abundance model and (because of computational limitations) 100 iterations of the occurrence model. We inferred significance of parameter estimates from the 95% bootstrapped confidence intervals (bCIs, Canty & Ripley 2014) and computed ANOVA tables using type III Wald tests (Fox & Weisberg 2011).

Where the minimum adequate model included significant trait × land use interactions, we evaluated the relative importance of land use, traits and their interactions. The following models were constructed for both species occurrence and abundance (if present):

1. Interactive model: the minimum adequate model
2. Additive model: as 1, but with all interactions removed
3. Traits model: as 2, but with all land-use variables removed
4. Land-use model: as 2, but with all trait variables removed
5. Null model: only random effects included.

The importance of interactive terms was assessed by comparing the additive model with the interactive model; the importance of traits versus land-use was assessed by comparison with the additive model. We chose not to use information criteria for these comparisons. Akaike's Information Criterion, with its low penalty per extra parameter (2 units), can overestimate the importance of predictors with more parameters when, as here, the dataset is large (Arnold 2010; Link & Barker 2006); whilst the penalty for the Bayesian Information Criterion (the log of the sample size) can be too stringent when, as here, the data are not independent (Jones 2011). Calculating appropriate penalty terms for complex mixed-effects models is far from straightforward (Delattre, Lavielle & Poursat 2014). We therefore assessed the relative importance of interactive effects in the minimum adequate models using marginal R^2_{GLMM} values (R^2 for mixed models), i.e., the variance explained by fixed effects alone (Barton 2013; Nakagawa & Schielzeth 2013). Specifically, we calculated the decrease in explanatory power when the predictor set of interest was excluded from the model (similar to the process for linear models in Ray-Mukherjee *et al.* 2014), as a percentage of the marginal R^2_{GLMM} when the predictor set was included. We used the same approach to estimate the importance of each trait and each land-use variable separately. These ‘unique’ contributions of focal predictors when isolated from other variables may under- or over-estimate the full contribution of the focal predictors, depending on the covariation among explanatory variables.

We performed a randomization test to ensure that differences in $\mathrm{R}^2{}_{\mathrm{GLMM}}$ values were not merely caused by differences in model complexity (Nakagawa & Schielzeth 2013). In each trial (1,000 for abundance models and 100 for occurrence models), we randomized the species names in the trait dataset, conserving the between-trait correlations and dataset structure, but breaking any link between traits and occurrence or abundance. We calculated marginal $\mathrm{R}^2{}_{\mathrm{GLMM}}$ values from interactive, additive and traits-only models fitted to the randomized data (the land-use-only and null models were unaffected by the randomization). We counted how often marginal $\mathrm{R}^2{}_{\mathrm{GLMM}}$ from the randomized data exceeded that of the original models, and expressed the difference as a z-score. If interactive models are favored simply because they have more parameters (i.e. a bias caused by an incorrect penalty for complexity), the observed marginal $\mathrm{R}^2{}_{\mathrm{GLMM}}$ will be approximately the average of the values across randomizations.

All analyses were carried out using R: A Language and Environment for Statistical Computing version 2.15.3 (R Core Team 2013).

Results

Model results

Many trait × land use interactions were retained after model simplification, explaining a significant amount of variation in both species occurrence and abundance if present (Tables 2 and 3, see Table S4.1 and 4.2 for full coefficients). Effects of trait × land use interactions were often different for species occurrence and abundance. A decrease in the number of species might enable remaining species to persist at higher abundances (Newbold *et al.* 2014).

[Table 2 about here.]

[Table 3 about here.]

Importance of trait × pressure interactions

Models where interactions were excluded (additive models) explained 13% and 37% less variation in occurrence and abundance respectively, than the interactive models did (marginal R^2_{GLMM}, Table 4). Traits were relatively more important than land use. The traits-only model explained 85% and 70% as much variation in occurrence and abundance, respectively, as the additive model, while land-use-only models only explained 9% and 17% as much variation in occurrence and abundance as the additive model (marginal R^2_{GLMM}, Table 4). These results are not an artifact of model complexity. The observed occurrence models had higher marginal R^2_{GLMM} than every randomization (z scores: trait-only model = 19.87; additive—traits and land use—model = 19.77; interactive model = 15.53). The observed abundance models outperformed every randomization for the interactive model (z = 4.69), and 97% of the additive (z = 4.49) and trait-only models (z = 5.09).

Including traits increased models' marginal $R^2\ _{\mathrm{GLMM}}$ (variance explained by fixed effects), but the conditional $R^2\ _{\mathrm{GLMM}}$ values (variance explained by fixed and random effects) change less, because the effect of traits can also be explained as taxonomic differences in the random-effects structure (Table 4, Table S4.3).

[Table 4 about here.]

Importance of variables

Interactions between LUI and traits were more important than interactions between mNDVI and traits (Fig. 1); we therefore focus on the former in the main text (see Supporting Information S4.1 for full mNDVI results).

[Figure 1 about here.]

In human dominated land-uses, species with shorter flight seasons were associated with lower probabilities of occurrence than species with longer flight seasons, although the magnitude of the relationship varied among land uses (Fig. 2). Among species that were present, shorter flight seasons were associated with lower abundances in all land uses, except for minimally-used cropland (Fig. 2).

[Figure 2 about here.]

Other traits were less important in determining species' occurrence and abundance (Fig. 1), but still had significant effects on species sensitivity (Tables 2 and 3). Species with smaller ITD were particularly sensitive to intensively-used cropland (estimate = 0.11, bCIs:0.02,0.18). Oligolectic, solitary, univoltine, long-tongued and nest-excavating species were less likely to be present in human-dominated land uses relative to secondary vegetation, particularly in intensively-used cropland and urban areas (Fig. 3). If present, however, the abundances of these species did not differ strongly from secondary vegetation (Fig. 4a).

Species with narrower dietary breadths (obligately oligolectic) were generally more sensitive to land use than dietary generalists (Fig. 3a, c, d). Short-tongued species were sensitive to some land uses in terms of probability of presence (Fig. 3e) but, if present, increased in abundance in some cases (Fig. 4c).

The effects of ecological traits on species' sensitivity were not always consistent across land uses. For example, species that were not obligately solitary were more sensitive than solitary species to lightly-used cropland (Fig. 3b), but less sensitive to pasture.

[Figure 3 about here.]

[Figure 4 about here.]

Discussion

Land-use change and intensification are considered to be major pressures on European bees (Ollerton *et al.* 2014; Potts *et al.* 2010). However, our analyses of 257 species at 1,584 sites suggest that these pressures alone explain little of the variation in the presence and abundance of bee species, as effects are often indirect (through reduced floral and nesting resources) and are masked by heterogeneity in species' responses (Roulston & Goodell 2011). We show that species' functional traits—phenology, foraging range, niche breadth and reproductive strategy (sociality)—influence their sensitivity to human-dominated land use, but do so in ways that differ among cropland, pastoral and urban habitats.

Land-use effects on species persistence and abundance

The probability of presence for most species was strongly reduced in intensively-used cropland relative to secondary vegetation, except for pollen generalists (polylectic, flexible or parasitic species); maintaining stable nesting habitats as well as floral resources may therefore help conserve diversity in such systems (Forrest *et al.* 2015). Species with shorter flight seasons—the most important trait in explaining occurrence and abundance patterns (Fig. 1)—were less likely to be present, and were at lower abundance, in intensively-used cropland, perhaps as this trait confers a higher risk of asynchrony with key floral resources. These results are consistent with previous findings in butterflies, that floral specialists with shorter flight seasons are more likely to be rare and threatened (Barbaro & van Halder 2009; Dennis *et al.* 2004). Previous studies of bees show less consistent patterns, although they assessed relatively few sites and species (e.g. Connop *et al.* 2010; Vázquez & Simberloff 2002). Although our analyses are based on different datasets, these results are similar to those in Williams *et al* (2010), which found that social species and pollen specialists were particularly sensitive to agricultural intensification.

Small species were also particularly sensitive to intensive agriculture, perhaps because larger species are able to forage further from their nest (Greenleaf *et al.* 2007; Wright, Roberts & Collins 2015). These results suggest that the placement of floral margins will need careful planning with respect to species' nesting habitats (Wright, Roberts & Collins 2015). Long-distance foraging may increase susceptability to some landscape-scale threats (e.g. pesticide exposure), but local conditions are likely to be more important for bee diversity and pollination services in temperate systems (Benjamin, Reilly & Winfree 2014; Kennedy *et al.* 2013).

Even in lightly-used cropland, short-tongued species that are not obligately solitary had significantly lower probability of occurrence relative to secondary vegetation, perhaps because their greater foraging breadth and capacity exposes them more to pesticides (Williams *et al.* 2010). In contrast, minimally-used cropland maintained diverse bee communities—although species with shorter flight seasons were still vulnerable—suggesting an advantage of organic and other low-intensity farming practices.

Many species were sensitive to pasture, except for social, polylectic, cavity-nesting species with long-flight seasons. Social and polylectic species have enhanced foraging capacity, enabling effective exploitation of available resources and persistence in a patchy mosaic. Small species were also less sensitive to pasture than to other land-uses, perhaps because forage is available within smaller distances of nesting sites.

Most species, including those with shorter flight seasons, were less likely to be present in urban areas than in secondary vegetation; only cavity-nesting species were unaffected. If present, however, most species tended to be fairly abundant, especially short-tongued species. Our results are congruent with previous studies that have found a negative impact of urbanisation on bees (Hernandez, Frankie & Thorp 2009) accompanied by an increase in the number of cavity-nesting species (Fortel *et al.* 2014; Hernandez, Frankie & Thorp 2009). Although other studies have found little difference in diversity between urban areas and semi-natural habitats (Baldock *et al.* 2015), our results suggest that further loss of secondary vegetation as a result of urbanization may be particularly detrimental to bee communities and to pollination services, as the loss of dietary generalists can greatly affect plant-pollinator networks (Memmott, Waser & Price 2004).

Limitations of the study

Our dataset is large, but only contains 12.5% of European bee species, with biases towards Western Europe and bumblebees. In addition, little of the variation in species' diversity was explained by fixed effects in our models: most was attributed to heterogeneity between sources

(Table S4.3), reflecting differences in sampling methodology, intensity and timing, as well as land-use practices or pressures that we did not consider. In addition, we used a small number of species' functional traits that were coarsely categorized and omitted intraspecific variation. Further collation of relevant trait information could greatly enhance the predictive ability of models such as these.

Some effects may be influenced by differential detectability; for instance, larger species that are active for longer are more likely to be sampled. This is in part why we have focussed on differences in sensitivity—changes between secondary vegetation and human-dominated land uses—rather than absolute differences in occurrence and abundance between species. However, detectability may vary among land uses. For instance, with visual sampling methods such as aerial transects, small species may be less frequently sampled in denser vegetation where they are more difficult to see. This may be in part accounted for by the inclusion of mNDVI in our models (as NDVI correlates with net primary productivity), but it is still important to consider possible effects of sampling bias on analyses such as these.

Conclusion

We have presented the most comprehensive analysis to date of how ecological traits affect bee species' responses to human impacts in Europe. Our results suggest that conservation and management activities should not simply focus on particular land uses or particular traits, but how they interact. Our findings have implications for ecosystem services and food security for two reasons. First, many of the traits analyzed influence pollination efficiency (de Bello *et al.* 2010). Second, trait-based vulnerability of species also reduces functional diversity (Forrest *et al.* 2015), which is important for insurance against disturbances, pollination efficiency (Albrecht *et al.* 2012) and stability under climate change (Bartomeus *et al.* 2013b). However, to fully understand the implications for pollination provision, further data on how traits influence pollination efficacy are required.

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Data accessibility

The majority of data included in this analysis will be published as part of the PREDICTS database (Hudson *et al.*, in preparation; metadata are already published in Hudson *et al.* 2014) and will be hosted by the Natural History Museum's Data Portal (http://data.nhm.ac.uk). Other data are owned by the data collectors.

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Tables

Table 1: Ecological trait data (after coarsening) available for European bee species. Numbers in parentheses indicate the number of species with these traits

Trait of interest	Proxy for trait of interest	Explanation
Niche Breadth	Lecty Status: Obligately oligolectic (63) Polylectic/Flexible (147) Species with no lecty status (47)	Obligately oligolectic species can be monolectic (foraging on one plant species) or oligolectic (forage on plants from <4 genera). Polylectic species are generalist foragers (collecting pollen from five or more plant genera) (Murray *et al.* 2009). Species that can be polylectic are placed within the latter group. Species with no lecty status are parasitic (they lay eggs in other species' nests) so do not collect pollen, but may respond more quickly to disturbance than other species, thus indicating the status of the total bee community (Sheffield *et al.* 2013).
	Tongue Length: Short (157) Long (100)	This is a family-specific trait; not the physical tongue length of each individual or species. It has been suggested that long-tongued bumblebees tend to forage on Fabaceae, and so are more specialized than short-tongued species (Goulson *et al.* 2005).
	Nesting Strategy: Excavators (141) Pre-existing cavity dwellers (116)	Excavators are species that excavate their own nests, often requiring bare hard ground or pithy stems; in this analysis, all species in this category nest below ground apart from one nesting above-ground in vegetation. Pre-existing cavity dwellers (e.g. bumblebees) nest above ground in pre-existing cavities such as empty snail shells, regardless of nest location, or are parasitic (Potts *et al.* 2005).
Phenology	Duration of the flight season: From two to twelve months (257)	Longer flight seasons increase the number of flowering species with which a bee overlaps. Flight season duration is calculated using the earliest and latest date in the year a specimen has ever been recorded; in reality, this is an overestimate as phenology depends on weather conditions that vary between years.

	Voltinism: Obligately univoltine (224) Multivoltine /Flexible (33)	Multivoltine species lay eggs multiple times throughout the year (most are bivoltine, laying twice), and so have a higher reproductive capacity than univoltine species which lay only one brood per year. Univoltine species may be particularly vulnerable to disturbances that coincide with the time of reproduction (Brittain & Potts 2011). Voltinism can vary with geography and the climate; species that can vary brood production depending on environmental conditions are classed as not obligately univoltine.
Reproductive strategy	Sociality: Obligately solitary (203) Not obligately solitary (54)	Social bees have a higher foraging and reproductive capacity, and have a faster response to resource provision, than solitary bees, which may buffer them against human impacts. However, sociality requires continuous brood production, which may increase time stress and resource requirements. Enhanced foraging capacity may also increase pesticide exposure (as foragers using various resources in different areas may bring pesticide-containing pollen and nectar back to the nest, Brittain & Potts 2011). Social species also tend to have low effective population sizes, which may make populations more susceptible to human impacts (Chapman & Bourke 2001).
Foraging distance	Inter-tegular distance (ITD): From one to six mm (257)	ITD is a proxy for dry weight (Cane 1987; Hagen & Dupont 2013) and foraging distance in bees (Greenleaf *et al.* 2007). Although alternative measures of body size do exist (e.g. wingspan), the relationship with foraging distance is either understudied or inconsistent among genera (Cane 1987; Westphal, Steffan-Dewenter & Tscharntke 2006). Only data for females were used.

Table 2: Anova table for minimum adequate model of probability of presence. Stars indicate the level of significance: <0.05*, <0.01**, <0.001***. The minimum adequate model had a marginal R^2_{GLMM} of 0.07 and a conditional R^2_{GLMM} of 0.578. Acronyms: LUI = Land-use and intensity, ITD = inter-tegular distance (body size), mNDVI = mean NDVI

Term	χ^2	Df	Sig
(Intercept)	52.19	1	***
LUI	64.71	5	***
mNDVI	28.39	1	***
Sociality	4.18	1	*
Lecty status	32.11	2	***
Tongue length guild	2.53	1	
Voltinism	0.32	1	
Duration of flight season	18.32	1	***
ITD	5.75	1	*
Nest construction	0.00	1	
LUI × Sociality	36.20	5	***
mNDVI × Sociality	16.90	1	***
LUI × Lecty status	66.39	10	***
mNDVI × Lecty status	31.20	2	***
LUI × Tongue length guild	11.33	5	*
mNDVI × Tongue length guild	7.75	1	**
LUI × Voltinism	48.66	5	***
LUI × Duration of flight season	43.81	5	***
mNDVI × Duration of flight season	5.30	1	*
LUI × ITD	45.15	5	***
mNDVI × ITD	12.18	1	***
LUI × Nest construction	25.23	5	***

Table 3: Anova table for minimum adequate model of abundance. Stars indicate the level of significance: <0.05*, <0.01**, <0.001***. The minimum adequate model had a marginal R^2_{GLMM} of 0.02 and a conditional R^2_{GLMM} of 0.72. Acronyms: LUI = Land-use and intensity, ITD = inter-tegular distance (body size), mNDVI = mean NDVI

Term	χ^2	Df	Sig
(Intercept)	0.37	1	
LUI	12.39	5	*
mNDVI	7.56	1	**
Sociality	4.36	1	*
Lecty status	7.92	2	*
Tongue length guild	11.45	1	***
Voltinism	1.37	1	
Duration of flight season	5.05	1	*
ITD	7.34	1	**
LUI × Sociality	23.76	5	***
mNDVI × Lecty status	9.13	2	*
LUI × Tongue length guild	12.16	5	*
mNDVI × Tongue length guild	21.55	1	***
LUI × Voltinism	40.02	5	***
LUI × Duration of flight season	17.14	5	**
mNDVI × ITD	12.35	1	***

Table 4: The fit to data of a null model, models with traits only and land-use only, and additive and interactive models with both land use and traits. NThe interactive model is the minimum adequate model. AIC may favor more complex models (Arnold 2010; Link & Barker 2006), but AIC weights are presented for comparison. Variance of taxonomic random effects are also given (species and species within family).

Response	Model name	Marginal R^2 GLMM	Conditional R^2 GLMM	AIC weights	Species variance	Species within family variance
Probability of presence	Null model	0.000	0.552	0.000	1.097	0.131
	Land use only	0.008	0.571	0.000	1.100	0.132
	Trait only	0.053	0.560	0.000	0.803	0.164
	Additive	0.058	0.577	0.000	0.805	0.166
	Interactive	0.067	0.579	1.000	0.830	0.162
Abundance of present species	Null model	0.000	0.692	0.000	0.116	0.018
	Land use only	0.004	0.694	0.000	0.116	0.019
	Trait only	0.010	0.696	0.000	0.102	0.033
	Additive	0.012	0.697	0.000	0.102	0.034
	Interactive	0.020	0.708	1.000	0.104	0.043

Figures

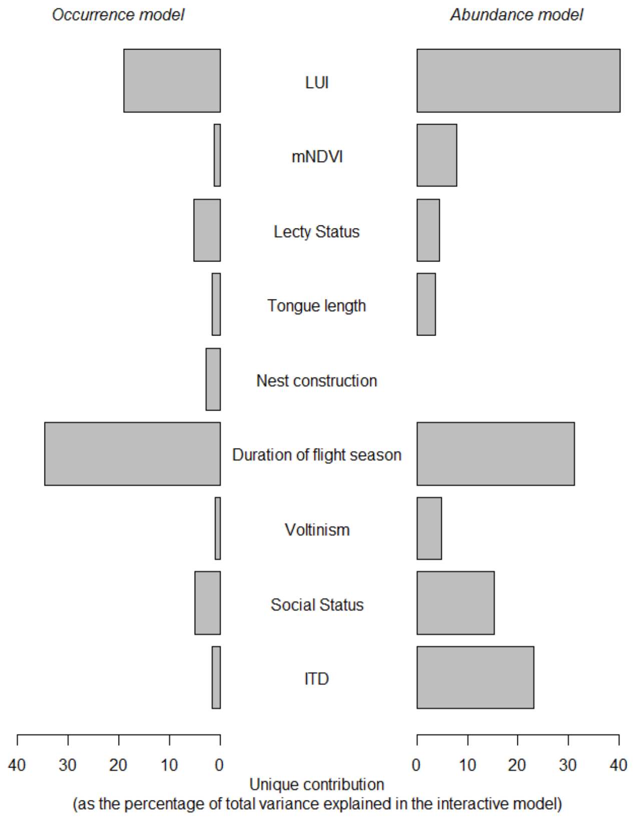


Figure 1: Unique contribution of variables to the explanatory power of minimum adequate models of occurrence and abundance. Contribution is reported as the reduction in variance explained by fixed effects (marginal $R^2{}_{\mathrm{GLMM}}$) when the variable and all its interactions are removed from the model, as a percentage of the total variation explained by fixed effects in the minimum adequate models

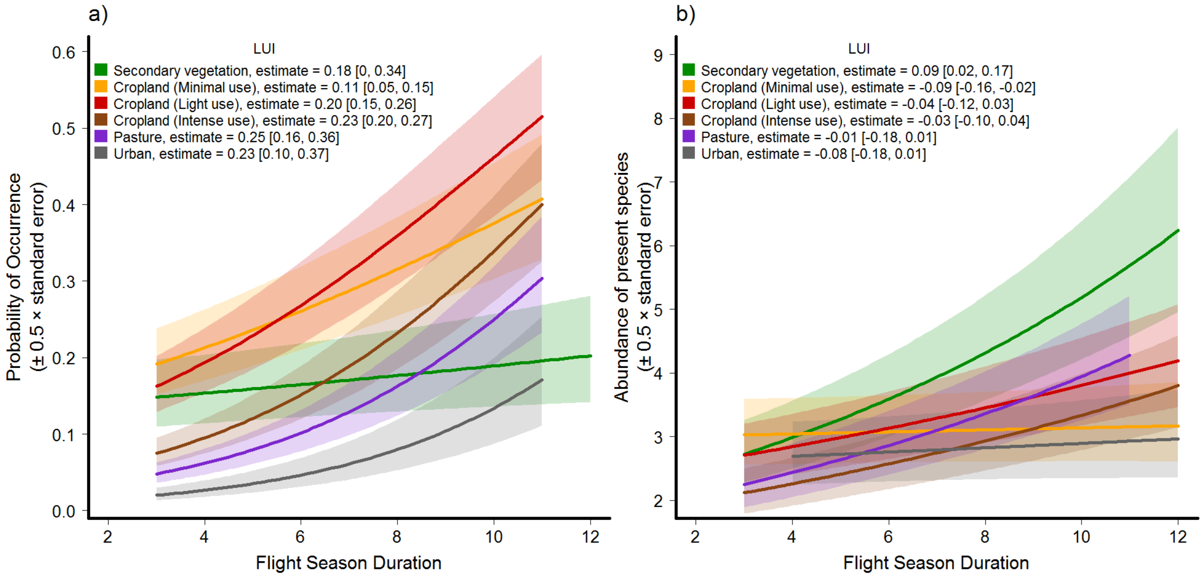


Figure 2: Relationship between flight season duration and a) probability of species presence and b) abundance of present species, in different habitat types, as estimated from the minimum adequate models. Error bars represent half the standard error, to ease comparison. The legend indicates the coefficient estimate extracted from the model with 95% bootstrapped confidence intervals (bCIs) in parentheses. The coefficients for human-dominated land-uses are the difference in slope between the given land use and that of secondary vegetation. If bCIs do not cross zero, the estimate is taken to be significant.

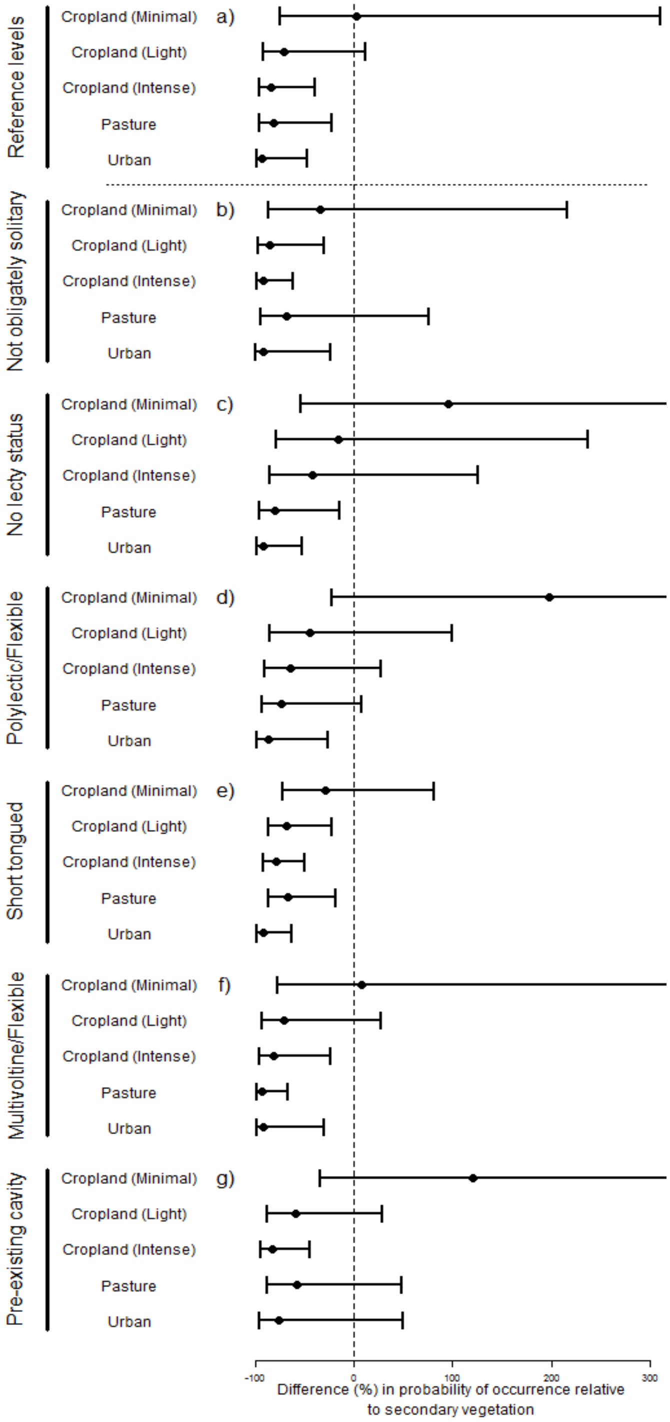


Figure 3: Land use and intensity (LUI) impact on species with differing (categorical) ecological traits. For each trait level, this is shown as the % difference in probability of occurrence relative to secondary vegetation, with 95% confidence intervals (CIs) calculated from the model. The trait reference levels in the models were oligolectic, solitary, univoltine, long-tongued, and nest excavating species. The effect of LUI on species with these trait values is presented in panel a, and the effects on species with other trait values in panels b-g. Therefore, to compare the sensitivity of long-tongued species and short-tongued species to LUI, one would compare panels a and e. CIs in some panels extend beyond the plot region.

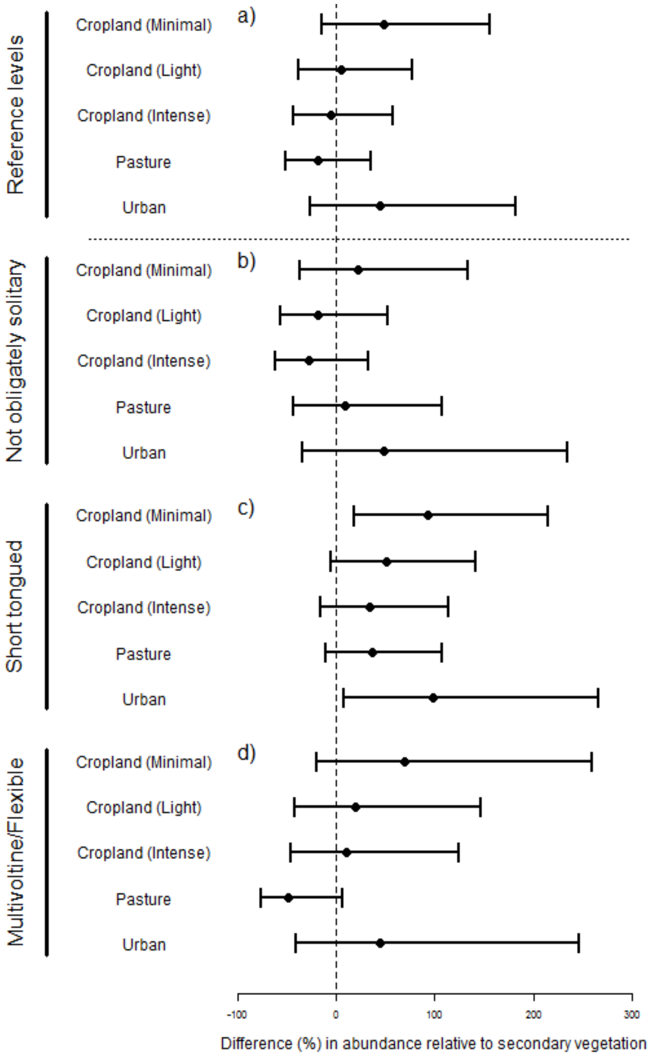


Figure 4: Land use and intensity (LUI) impact on species with differing (categorical) ecological traits. For each trait level, this is shown as the % difference in abundance relative to secondary vegetation, with 95% confidence intervals calculated from the model. The trait reference levels in the model included oligolectic, solitary, univoltine, long-tongued species. The effect of LUI on species with these trait values is presented in panel a, and the effects of species with other trait values in panels b-d. Therefore, to compare the sensitivity of long-tongued species and short-tongued species to LUI, one would compare panels a and c.

Appendix S1: Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes.

Supporting Information

S1 Diversity Dataset

Table S1.1: Terms used to search the Web of Science database for papers potentially containing useful data.

	Web of Knowledge search terms
1	"(arthropod* OR bee* OR pollinat*) AND (abundance OR diversity) AND (agricultur* OR anthropogenic OR land use OR threat)"
2	"pollinat* AND land-use AND diversity"
3	"pollinat* habitat abundance*"
4	"pollinat* threat"
5	"pollinat* agricultur*"

Table S1.2: Data sources and sample sizes

Reference	Study ID	Country	Sampling years	Number of sites	Number of taxa
Quaranta *et al.* (2004)	Quaranta2004 Pisa	Italy	2000 - 2000	2	28
Meyer, Gaebele & Steffan-Dewenter (2007)	Meyer2007 2000data	Germany	2000 - 2000	15	7
Darvill, Knight & Goulson (2004)	Darvill2004 transect	United Kingdom	2001 - 2001	17	2
Diekötter *et al.* (2006)	Diekoetter2006 grid	Germany	2001 - 2001	115	2
Billeter *et al.* (2007)	Greenveins2001 CzechRepublic01	Czech Republic	2001 - 2001	32	33
	Greenveins2001 Germany01	Germany	2001 - 2001	64	69
	Greenveins2001 Switzerland01	Switzerland	2001 - 2001	80	50
	Greenveins2001 Estonia01	Estonia	2001 - 2001	64	26
	Greenveins2001 Belgium01	Belgium	2001 - 2001	64	22
	Greenveins2001 Netherlands01	Netherlands	2001 - 2001	64	9

	Greenveins2001 Germany02	Germany	2002 - 2002	64	127
	Greenveins2001 France02	France	2002 - 2002	48	54
	Greenveins2001 Belgium02	Belgium	2002 - 2002	64	59
	Greenveins2001 Netherlands02	Netherlands	2002 - 2002	64	40
	Greenveins2001 CzechRepublic02	Czech Republic	2002 - 2002	32	80
	Greenveins2001 Estonia02	Estonia	2002 - 2002	64	61
	Greenveins2001 Switzerland02	Switzerland	2002 - 2002	121	92
Marshall, West & Kleijn (2006)	Marshall2006 sweepnet	United Kingdom	2003 - 2003	42	25
	Marshall2006 transect	United Kingdom	2003 - 2003	42	25
Albrecht *et al.* (2010)	Albrecht2010 sweepnet	Switzerland	2003 - 2004	101	51
	Albrecht2010 transect	Switzerland	2003 - 2004	101	57
Hanley (2005)	Hanley2005 unpublished	United Kingdom	2004 - 2005	6	10
Öckinger & Smith (2007)	Ockinger2007 transect	Sweden	2004 - 2004	36	10
Kohler *et al.* (2008)	Kohler2008 pantrap	Netherlands	2004 - 2004	5	4
Kohler *et al.* (2008)	Kohler2008 sight	Netherlands	2004 - 2004	5	12

Kohler *et al.* (2008)	Kohler2008 windowtrap	Netherlands	2004 - 2004	5	6
Knight *et al.* (2009)	Knight2009 b.pascuorum	United Kingdom	2004 - 2004	7	1
Herrmann *et al.* (2007)	Herrmann2007 Abundance	Germany	2005 - 2005	13	1
	Herrmann2007 Colonynumber	Germany	2005 - 2005	13	1
Meyer, Gaebele & Steffan-Dewenter (2007)	Meyer2007 2005data	Germany	2005 - 2005	15	8
Franzén & Nilsson (2008)	Franzen2009 transect	Sweden	2005 - 2005	16	77
Kohler *et al.* (2008)	Kohler2008 naturereserve	Netherlands	2005 - 2005	4	11
Connop *et al.* (2011)	Connop2009 colonies	United Kingdom	2005 - 2005	5	2
Goulson, Lye & Darvill (2008)	Goulson2008 mountains	Poland	2006 - 2006	32	22
Goulson *et al.* (2010)	Goulson2010 nestdensity	United Kingdom	2007 - 2007	14	2
Hanley *et al.* (2011)	Hanley2011 bumblebee	United Kingdom	2007 - 2010	34	5
Holzschuh *et al.* (2011)	Holzschuh2011 abundance	Germany	2007 - 2007	67	1
Weiner *et al.* (2011)	Weiner2011 flowervisitorweb	Germany	2007 - 2007	29	49
Redpath *et al.* (2010)	Redpath2010 bumblebees	United Kingdom	2008 - 2008	11	5
Blake *et al.* (2011)	Blake bumblebee2008	United Kingdom	2008 - 2008	2	6
Schüepp *et al.* (2011)	Schuepp2011 hymenoptera	Switzerland	2008 - 2008	30	7

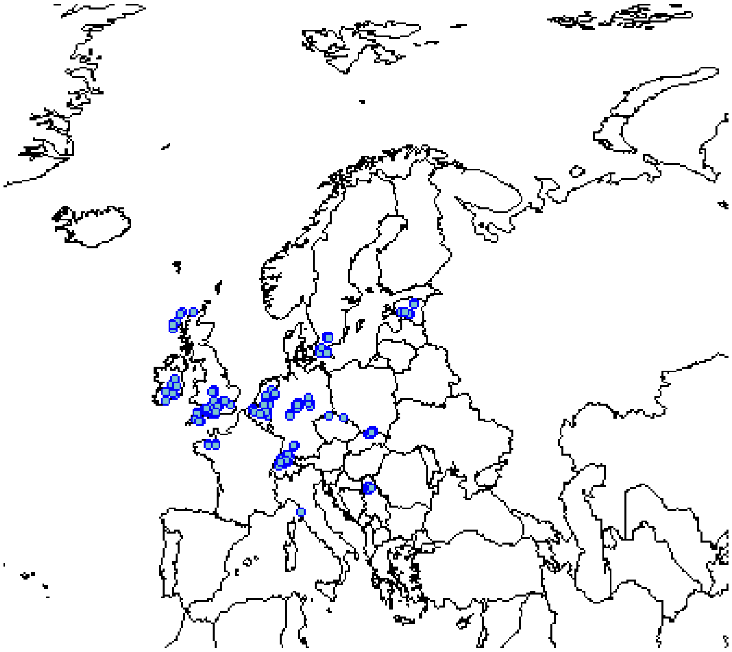
Bates *et al.* (2011)	Bates2011 multipletraps	United Kingdom	2009 - 2010	24	57
Blake *et al.* (2011)	Blake bumblebee	United Kingdom	2009 - 2010	4	6
Power & Stout (2011)	Power2011 transect	Ireland	2009 - 2009	20	6
Samnegård, Persson & Smith (2011)	Samnegard2011 pantrap	Sweden	2009 - 2009	9	31
Osgathorpe, Park & Goulson (2012)	Osgathorpe2012 Hebrides	United Kingdom	2009 - 2009	23	10
Verboven, Brys & Hermy (2012)	Verboven2012 bumblebees	Belgium	2009 - 2009	9	4
Osgathorpe, Park & Goulson (2012)	Osgathorpe2012 Somerset	United Kingdom	2010 - 2010	22	10
Hanley (2011)	Hanley2011 Whitchurch	United Kingdom	2011 - 2011	8	17
Mudri-Stojnić *et al.* (2012)	Mudri pollinators	Serbia	2011 - 2011	16	19

Table S1.3: Land-use class and intensity definitions as used in Hudson *et al.* (2014)

Level 1 Land Use	**Predominant Land Use**	**Minimal use**	**Light use**	**Intense use**
No evidence of prior destruction of the vegetation	**Primary forest**	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that is severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
	Primary Non-Forest	As above	As above	As above
Recovering after destruction of the vegetation	**Mature Secondary Vegetation**	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Intermediate Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Young Secondary Vegetation	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
	Secondary Vegetation (indeterminate age)	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use

Human use (agricultural)	**Plantation forest**	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently ($<$ 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent ($<$ 20 years) clear-felling. Monoculture oil-palm plantations with no recent ($<$ 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input.Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent ($<$ 20 years) clear-felling.
	Cropland	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
	Pasture	Pasture with minimal input of fertiliser and pesticide, and with low stock density (*not* high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, *and* with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).
Human use (urban)	**Urban**	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.

Figure S1.1: Sites across Europe for which we have bee species occurrence or abundance measurements.



S2 Species traits dataset

S2.1 Species list, based on taxonomy from Michener (2000)

Amegilla albigena

Andrena agilissima

Andrena alfkenella

Andrena angustior

Andrena anthrisci

Andrena barbilabris

Andrena bicolor

Andrena bucephala

Andrena carantonica

Andrena chrysopus

Andrena chrysosceles

Andrena cineraria

Andrena cinerea
Andrena clarkella
Andrena coitana
Andrena combinata
Andrena congruens
Andrena curvungula
Andrena decipiens
Andrena denticulata
Andrena distinguenda
Andrena dorsata
Andrena enslinella
Andrena flavipes
Andrena florea
Andrena floricola
Andrena florivaga
Andrena fucata
Andrena fulva
Andrena fulvata
Andrena fulvida
Andrena fuscipes
Andrena gravida
Andrena haemorrhoa
Andrena hattorfiana
Andrena helvola
Andrena humilis
Andrena labialis
Andrena labiata
Andrena lagopus
Andrena lapponica
Andrena lathyri
Andrena minutula
Andrena minutuloides
Andrena mitis
Andrena nigroaenea
Andrena nigroolivacea
Andrena nigrospina
Andrena nitida
Andrena niveata
Andrena ovatula
Andrena pandellei
Andrena pilipes
Andrena praecox
Andrena proxima
Andrena ruficrus
Andrena semilaevis
Andrena similis
Andrena strohmella
Andrena subopaca
Andrena synadelpha
Andrena tarsata
Andrena tibialis
Andrena trimmerana
Andrena vaga
Andrena varians
Andrena ventralis
Andrena viridescens
Andrena vulpecula
Andrena wilkella

Anthidiellum strigatum

Anthidium manicatum

Anthophora aestivalis

Anthophora dispar

Anthophora furcata

Anthophora plumipes

Anthophora retusa

Apis mellifera

Bombus barbutellus

Bombus bohemicus

Bombus campestris

Bombus cryptarum

Bombus distinguendus

Bombus hortorum

Bombus humilis

Bombus hypnorum

Bombus jonellus

Bombus lapidarius

Bombus lucorum

Bombus magnus

Bombus muscorum

Bombus norvegicus

Bombus pascuorum

Bombus pomorum

Bombus pratorum

Bombus pyrenaeus

Bombus quadricolor

Bombus ruderarius

Bombus ruderatus

Bombus rupestris

Bombus schrencki

Bombus semenoviellus

Bombus soroeensis

Bombus subterraneus

Bombus sylvarum

Bombus sylvestris

Bombus terrestris

Bombus vestalis

Bombus veteranus

Bombus wurflenii

Ceratina cucurbitina

Chelostoma campanularum

Chelostoma distinctum

Chelostoma florisomne

Chelostoma rapunculi

Coelioxys inermis

Coelioxys rufescens

Colletes cunicularius

Colletes daviesanus

Colletes succinctus

Dasypoda hirtipes

Dufourea dentiventris

Eucera eucnemidea

Eucera longicornis

Eucera nigrescens

Halictus confusus

Halictus gemmeus

Halictus maculatus

Halictus rubicundus
Halictus scabiosae
Halictus simplex
Halictus subauratus
Halictus tumulorum
Heriades truncorum
Hoplitis adunca
Hoplitis anthocopoides
Hoplitis claviventris
Hoplitis leucomelana
Hylaeus angustatus
Hylaeus annularis
Hylaeus brevicornis
Hylaeus communis
Hylaeus confusus
Hylaeus difformis
Hylaeus gibbus
Hylaeus gredleri
Hylaeus hyalinatus
Hylaeus nigritus
Hylaeus paulus
Hylaeus punctatus
Hylaeus rinki
Hylaeus signatus
Hylaeus sinuatus
Hylaeus styriacus
Hylaeus variegatus
Lasioglossum albipes
Lasioglossum albocinctum
Lasioglossum brevicorne
Lasioglossum calceatum
Lasioglossum costulatum
Lasioglossum fulvicorne
Lasioglossum glabriusculum
Lasioglossum interruptum
Lasioglossum laevigatum
Lasioglossum laticeps
Lasioglossum lativentre
Lasioglossum leucopus
Lasioglossum leucozonium
Lasioglossum lineare
Lasioglossum lucidulum
Lasioglossum majus
Lasioglossum malachurum
Lasioglossum minutissimum
Lasioglossum minutulum
Lasioglossum morio
Lasioglossum nigripes
Lasioglossum nitidiusculum
Lasioglossum nitidulum
Lasioglossum pallens
Lasioglossum parvulum
Lasioglossum pauxillum
Lasioglossum politum
Lasioglossum puncticolle
Lasioglossum quadrinotatum
Lasioglossum rufitarse
Lasioglossum sexnotatum

Lasioglossum sexstrigatum

Lasioglossum smeathmanellum

Lasioglossum subfasciatum

Lasioglossum villosulum

Lasioglossum xanthopus

Lasioglossum zonulus

Macropis europaea

Macropis fulvipes

Megachile alpicola

Megachile centuncularis

Megachile circumcincta

Megachile ericetorum

Megachile ligniseca

Megachile versicolor

Megachile willughbiella

Melecta albifrons

Melitta haemorrhoidalis

Melitta leporina

Melitta nigricans

Melitta tricincta

Nomada alboguttata

Nomada armata

Nomada bifasciata

Nomada castellana

Nomada fabriciana

Nomada ferruginata

Nomada flava

Nomada flavoguttata

Nomada flavopicta

Nomada fucata

Nomada fulvicornis

Nomada goodeniana

Nomada hirtipes

Nomada lathburiana

Nomada leucophthalma

Nomada marshamella

Nomada panzeri

Nomada ruficornis

Nomada rufipes

Nomada sheppardana

Nomada signata

Nomada striata

Nomada succincta

Nomada zonata

Osmia aurulenta

Osmia bicolor

Osmia bicornis

Osmia brevicornis

Osmia caerulescens

Osmia leaiana

Osmia parietina

Osmia spinulosa

Osmia uncinata

Panurgus banksianus

Panurgus calcaratus

Rhodanthidium septemdentatum

Rophites quinquespinosus

Sphecodes albilabris

Sphecodes crassus

Sphecodes ephippius

Sphecodes ferruginatus

Sphecodes geoffrellus

Sphecodes gibbus

Sphecodes hyalinatus

Sphecodes miniatus

Sphecodes monilicornis

Sphecodes pellucidus

Sphecodes scabricollis

Sphecodes spinulosus

Tetralonia malvae

Trachusa byssina

Table S2.1: Original and coarsened factor levels of species traits

Trait	Coarsened factor levels	Original levels	Rationale
Nesting trait	Excavators	Excavators in the soil or vegetation	This trait was coarsened to represent two distinct nesting strategies: those that build their own holes versus those that don't. Excavators are particular about nesting sites, often requiring hard, bare ground or pithy stems, whilst those that don't excavate use existing cavities or old nesting sites, regardless of nest location.
	Non-excavators	Carder bees, renters, masons, cleptoparasites and social parasites	
Sociality	Obligately solitary	Solitary, solitary or communal, communal, cleptoparasitic	The sociality of the species was defined according to how their offspring are raised, because this relates to reproductive capacity. Social species, or those that raise their young in social nests (such as social parasites), are able to produce greater numbers of offspring because there are more workers to provision those offspring. Primitively eusocial species are able to adjust their reproductive capacity, often according to resource requirements: for example, *Halictus rubicundus* is social in warmer, more resource rich areas but solitary in other areas.
	Not obligately solitary	Highly eusocial, primitively eusocial, solitary/primitively eusocial, polymorphic, social parasites	
Lecty	No Lecty status	No Lecty status	Species with no lecty status are those which do not collect their own pollen, for example cleptoparasites. Phenotypic flexibility can be considered as a form of generalism so species that can be either oligolectic or polylectic are considered in the same category as the pollen generalists.

	Obligately oligolectic	Oligolectic	
	Polylectic/Flexible	Polylectic, oligolectic or polylectic	
Voltinism	Univoltine	Univoltine	Species were split into two categories: those with only one generation per year, and those that do have or can have more than one generation per year, as the latter are predicted to be less impacted by local threats
	Multivoltine/Flexible	Bivoltine, multivoltine, univoltine or bivoltine, univoltine or multivoltine	

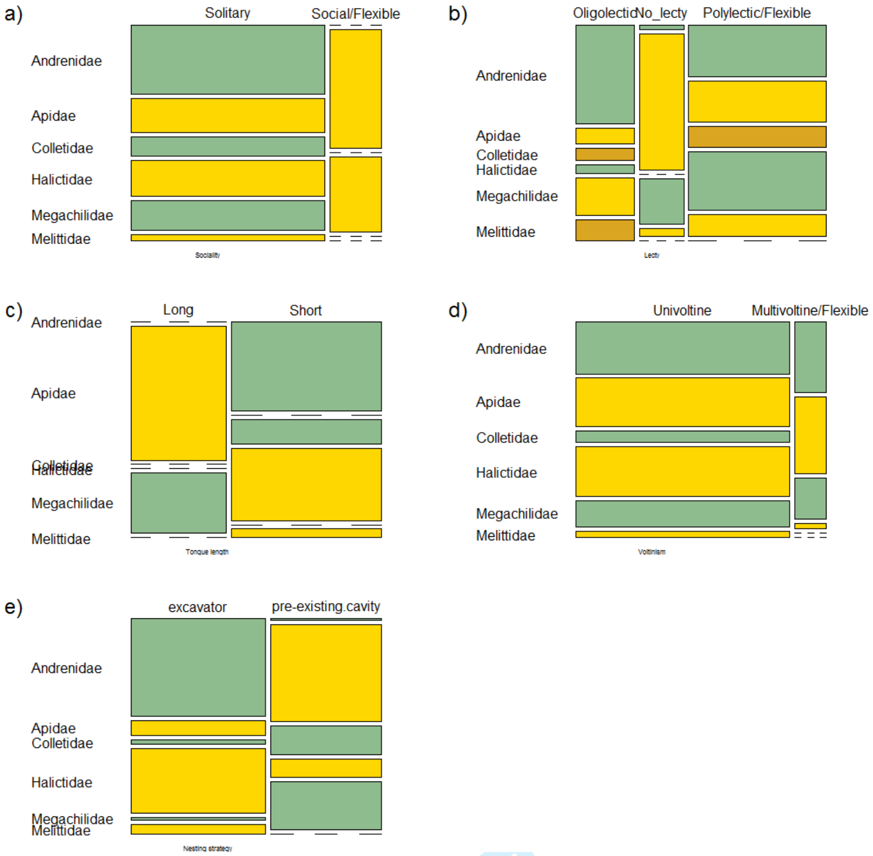


Figure S2.1: Mosaic plots showing the distribution across families of the following categorical traits: a) Sociality, b) Lecty status, c) Tongue length, d) Voltinism, and e) Nesting strategy.

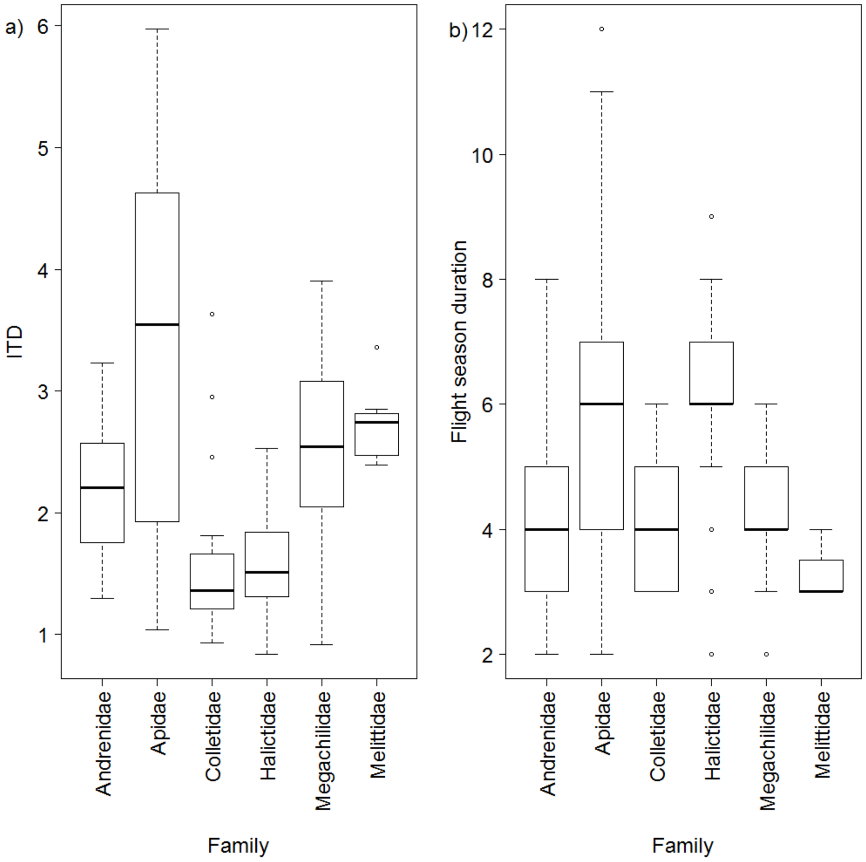


Figure S2.2: Mosaic plots showing the distribution across bee families of a) Inter-tegular distance (ITD) and b) Flight season duration.

S3 Model Checking

Table S3.1: Variance inflation factors for the dataset used to model probability of species occurrence. GVIF is the generalized variance inflation factor. DF is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables. None of the variables were removed during backwards stepwise model simplification so the GVIFs here are applicable both to the maximal and minimum adequate model for probability of species occurrence.

Explanatory Variable	GVIF	Df	GVIF$^($0.5Df)
LUI	1.22	5	1.02
mNDVI	1.19	1	1.09
ITD	2.66	1	1.63
Nest construction	4.38	1	2.09
Sociality	1.96	1	1.40
Lecty status	1.85	2	1.17
Voltinism	1.27	1	1.13
Tongue length guild	5.52	1	2.35
Duration of flight season	1.88	1	1.37

Table S3.2: Variance inflation factors for the dataset used to model abundance of present species, before model simplification. GVIF is the generalized variance inflation factor. DF is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables.

Explanatory Variable	GVIF	Df	GVIF$^{(}0.5Df)$
LUI	1.33	5	1.03
mNDVI	1.28	1	1.13
ITD	2.98	1	1.73
Nest construction	8.65	1	2.94
Sociality	2.58	1	1.61
Lecty status	1.90	2	1.17
Voltinism	1.60	1	1.26
Tongue length guild	9.60	1	3.10
Duration of flight season	2.83	1	1.68

Table S3.3: Variance inflation factors for the dataset used to model abundance of present species, after backwards stepwise model simplification based on likelihood ratio tests. GVIF is the generalized variance inflation factor. DF is the degrees of freedom. GVIF scaled by the degrees of freedom gives an indication of how much the standard errors are likely to be inflated due to collinearity between explanatory variables.

Explanatory Variable	GVIF	Df	GVIF$^{(}0.5Df)$
LUI	1.31	5	1.03
mNDVI	1.28	1	1.13
ITD	2.96	1	1.72
Sociality	2.58	1	1.61
Lecty status	1.68	2	1.14
Voltinism	1.59	1	1.26
Tongue length guild	3.64	1	1.91
Duration of flight season	2.82	1	1.68

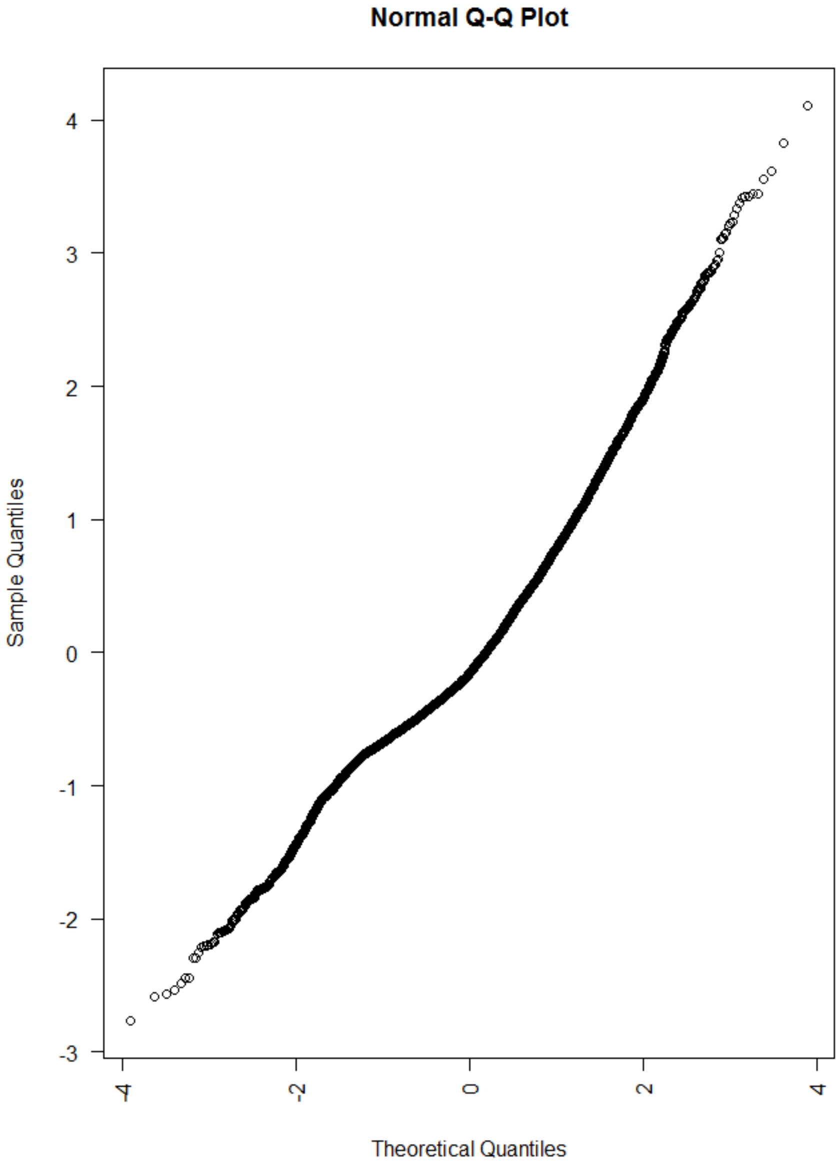


Figure S3.1: Q-Q plot to asssess residuals in the log-transformed abundance model for normality.

S4 Model Results

The following coefficient tables are the model outputs (estimate and standard errors) from mixed effects models in R statistical software. These are treatment contrasts, i.e, differences are given between each level and the reference level (oligolectic, solitary, univoltine, short-tongued species in secondary vegetation). The predicted mean of the response variable can be calculated from these tables. For interactions between categorical traits, we can calculate the probability of occurrence of a given trait level in a given land-use class, as a percentage of the probability of occurrence for that same trait level in secondary vegetation. Similarly, this can be done for the abundance of present species. These percentages are provided in the final column of the following coefficients table. Such calculations are not as meaningful for continuous variables, so are not given (denoted by a dash).

Table S4.1: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (bias, standard error, confidence intervals) for the model of species occurrence. Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero. The first level of each factor forms part of the intercept terms and so do not explicitly appear in the coefficients table (oligolectic, solitary, univoltine, long-tongued, nest excavating species in secondary vegetation). For each trait level and land-use combination, we also show the probability of species presence as a percentage of the probability of presence for that same trait level in secondary vegetation.

Variable	Coefficient	Original estimate	Standard error	Bias	bootstrapped Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval		Difference (%) in Probability of occurrence for trait level in given land use, relative to secondary vegetation
Intercept	(Intercept)	-6.42	1.14	-0.00	0.73	-7.98	-4.51	*	-
LUI	Cropland (Minimal use)	0.02	0.71	-0.01	0.25	-0.49	0.51		2
LUI	Cropland (Light use)	-1.22	0.68	0.01	0.27	-1.79	-0.59	*	-71
LUI	Cropland (Intense use)	-1.81	0.67	0.01	0.20	-2.18	-1.36	*	-84
LUI	Pasture	-1.69	0.73	-0.10	0.54	-2.89	-0.67	*	-82
LUI	Urban	-2.61	1.00	0.02	0.84	-4.23	-0.88	*	-93
mNDVI	mNDVI	7.61	1.21	0.01	0.78	5.96	9.08	*	-
Social Status	Not obligately solitary	-0.61	0.43	-0.05	0.38	-1.57	0.12		-
Lecty Status	No lecty status	2.41	0.77	-0.02	0.50	1.29	3.46	*	-
Lecty Status	Not obligately oligolectic	2.52	0.60	-0.02	0.34	1.93	3.26	*	-
Tongue length	Short tongue	0.82	0.72	-0.04	0.53	-0.45	1.90		-
Voltinism	Not obligately univoltine	0.00	0.28	-0.06	0.25	-0.53	0.58		-
Flight season duration	Flight season duration	0.18	0.09	-0.00	0.08	-0.00	0.34		-
ITD	ITD	0.39	0.16	0.02	0.11	0.18	0.64	*	-
Nest construction	Pre-existing cavity dweller	-0.55	0.49	0.01	0.31	-1.16	0.10		-
LUI × Social Status	Cropland (Minimal use) × Not obligately solitary	-0.44	0.26	0.00	0.15	-0.71	-0.13	*	-34
LUI × Social Status	Cropland (Light use) × Not obligately solitary	-0.65	0.25	0.00	0.13	-0.90	-0.34	*	-85
LUI × Social Status	Cropland (Intense use) × Not obligately solitary	-0.62	0.25	-0.00	0.12	-0.86	-0.36	*	-91
LUI × Social Status	Pasture × Not obligately solitary	0.54	0.33	-0.03	0.35	-0.06	1.25		-68
LUI × Social Status	Urban × Not obligately solitary	0.11	0.34	0.08	0.34	-0.64	0.83		-92
mNDVI × Social Status	mNDVI × Not obligately solitary	1.94	0.47	0.04	0.44	0.80	2.87	*	-
LUI × Lecty Status	Cropland (Minimal use) × No lecty status	0.65	0.47	0.03	0.21	0.19	1.12	*	92

LUI × Lecty Status	Cropland (Light use) × No lecty status	1.05	0.45	0.05	0.20	0.59	1.49	*	-16
LUI × Lecty Status	Cropland (Intense use) × No lecty status	1.26	0.44	0.02	0.17	0.92	1.64	*	-42
LUI × Lecty Status	Pasture × No lecty status	0.06	0.48	0.08	0.34	-0.61	0.83		-80
LUI × Lecty Status	Urban × No lecty status	0.09	0.66	0.09	0.58	-0.99	1.41		-92
LUI × Lecty Status	Cropland (Minimal use) × Not obligately oligolectic	1.07	0.35	0.00	0.14	0.82	1.39	*	187
LUI × Lecty Status	Cropland (Light use) × Not obligately oligolectic	0.62	0.33	0.02	0.13	0.36	0.95	*	-45
LUI × Lecty Status	Cropland (Intense use) × Not obligately oligolectic	0.78	0.32	-0.02	0.11	0.58	1.02	*	-64
LUI × Lecty Status	Pasture × Not obligately oligolectic	0.35	0.35	0.05	0.30	-0.23	1.01		-73
LUI × Lecty Status	Urban × Not obligately oligolectic	0.56	0.57	0.11	0.62	-0.56	2.23		-87
mNDVI × Lecty Status	mNDVI × No lecty status	-4.86	0.92	-0.07	0.56	-6.01	-3.74	*	-
mNDVI × Lecty Status	mNDVI × Not obligately oligolectic	-3.97	0.77	-0.02	0.46	-5.14	-3.06	*	-
LUI × Tongue length	Cropland (Minimal use) × Short tongue	-0.36	0.49	0.03	0.18	-0.68	0.08		-28
LUI × Tongue length	Cropland (Light use) × Short tongue	0.09	0.47	0.02	0.18	-0.30	0.57		-68
LUI × Tongue length	Cropland (Intense use) × Short tongue	0.24	0.46	0.01	0.14	-0.10	0.59		-79
LUI × Tongue length	Pasture × Short tongue	0.58	0.50	0.01	0.30	-0.04	1.19		-67
LUI × Tongue length	Urban × Short tongue	0.09	0.57	-0.01	0.48	-0.82	1.48		-92
mNDVI × Tongue length	mNDVI × Short tongue	-1.72	0.61	0.02	0.41	-2.41	-0.79	*	-
LUI × Voltinism	Cropland (Minimal use) × Not obligately univoltine	0.05	0.21	0.03	0.15	-0.25	0.41		7
LUI × Voltinism	Cropland (Light use) × Not obligately univoltine	-0.01	0.20	0.04	0.12	-0.23	0.33		-71
LUI × Voltinism	Cropland (Intense use) × Not obligately univoltine	0.10	0.20	0.03	0.11	-0.07	0.37		-82
LUI × Voltinism	Pasture × Not obligately univoltine	-1.02	0.24	-0.02	0.19	-1.44	-0.70	*	-93
LUI × Voltinism	Urban × Not obligately univoltine	0.14	0.26	0.04	0.22	-0.19	0.66		-91
LUI × Flight season duration	Cropland (Minimal use) × Flight season duration	0.11	0.05	0.00	0.02	0.05	0.15	*	-
LUI × Flight season duration	Cropland (Light use) × Flight season duration	0.20	0.05	0.00	0.02	0.15	0.26	*	-

LUI × Flight season duration	Cropland (Intense use) × Flight season duration	0.23	0.05	0.01	0.02	0.20	0.27	*	-
LUI × Flight season duration	Pasture × Flight season duration	0.25	0.06	0.00	0.05	0.16	0.36	*	-
LUI × Flight season duration	Urban × Flight season duration	0.23	0.08	-0.01	0.07	0.10	0.37	*	-
mNDVI × Flight season duration	mNDVI × Flight season duration	-0.23	0.10	0.00	0.08	-0.40	-0.07	*	-
LUI × ITD	Cropland (Minimal use) × ITD	-0.15	0.09	0.01	0.04	-0.24	-0.06	*	-
LUI × ITD	Cropland (Light use) × ITD	0.05	0.09	0.01	0.04	-0.03	0.12		-
LUI × ITD	Cropland (Intense use) × ITD	0.11	0.08	0.00	0.04	0.02	0.18	*	-
LUI × ITD	Pasture × ITD	-0.24	0.11	0.02	0.09	-0.41	-0.01	*	-
LUI × ITD	Urban × ITD	0.06	0.12	-0.02	0.09	-0.18	0.20		-
mNDVI × ITD	mNDVI × ITD	-0.67	0.19	-0.00	0.13	-0.96	-0.41	*	-
LUI × Nest construction	Cropland (Minimal use) × Pre-existing cavity dweller	0.77	0.46	0.01	0.17	0.41	1.15	*	121
LUI × Nest construction	Cropland (Light use) × Pre-existing cavity dweller	0.32	0.45	0.01	0.16	-0.05	0.71		-60
LUI × Nest construction	Cropland (Intense use) × Pre-existing cavity dweller	0.07	0.44	0.01	0.14	-0.15	0.46		-82
LUI × Nest construction	Pasture × Pre-existing cavity dweller	0.84	0.48	-0.01	0.34	0.21	1.66	*	-57
LUI × Nest construction	Urban × Pre-existing cavity dweller	1.20	0.54	0.04	0.48	0.35	2.29	*	-76

Table S4.2: Coefficient estimates (calculated using treatment contrasts in R statistics) and bootstrapped statistics (bias, standard error, confidence intervals) for the model of species abundance (when present). Significance is assumed if the bootstrapped 95% confidence intervals do not cross zero. The first level of each factor forms part of the intercept terms and so do not explicitly appear in the coefficients table (Oligolectic, Solitary, Univoltine, long-tongued species in secondary vegetation). For each trait level and land-use combination, we also show the species abundance as a percentage of the abundance for that same trait level in secondary vegetation.

Variable	Coefficient	Original estimate	Standard error	Bias	bootstrapped Standard error	Lower 95% Confidence Interval	Upper 95% Confidence Interval		Difference (%) in abundance for trait level in given land use, relative to secondary vegetation
Intercept	(Intercept)	-1.17	0.63	-0.00	0.62	-2.32	0.04		-
LUI	Cropland (Minimal use)	0.39	0.28	-0.01	0.27	-0.12	0.92		48
LUI	Cropland (Light use)	0.05	0.27	-0.01	0.27	-0.47	0.57		5
LUI	Cropland (Intense use)	-0.06	0.26	-0.01	0.27	-0.59	0.46		-6
LUI	Pasture	-0.21	0.26	-0.01	0.26	-0.75	0.28		-19
LUI	Urban	0.37	0.34	-0.02	0.35	-0.35	1.04		45
mNDVI	mNDVI	3.04	0.72	0.02	0.69	1.64	4.49	*	-
Social Status	Not obligately solitary	0.28	0.18	0.00	0.19	-0.10	0.65		-
Lecty Status	No lecty status	1.15	0.43	0.02	0.45	0.31	2.06	*	-
Lecty Status	Not obligately oligolectic	0.96	0.36	0.00	0.37	0.25	1.69	*	-
Tongue length	Short tongue	0.86	0.37	0.02	0.36	0.17	1.63	*	-
Voltinism	Not obligately univoltine	-0.10	0.18	0.00	0.18	-0.43	0.24		-
Flight season duration	Flight season duration	0.09	0.04	-0.00	0.04	0.02	0.17	*	-
ITD	ITD	0.23	0.08	0.00	0.08	0.06	0.39	*	-
LUI × Social Status	Cropland (Minimal use) × Not obligately solitary	-0.20	0.18	-0.00	0.18	-0.54	0.18		21
LUI × Social Status	Cropland (Light use) × Not obligately solitary	-0.26	0.17	-0.00	0.18	-0.60	0.11		-19
LUI × Social Status	Cropland (Intense use) × Not obligately solitary	-0.27	0.17	-0.00	0.17	-0.61	0.08		-28
LUI × Social Status	Pasture × Not obligately solitary	0.29	0.19	-0.00	0.20	-0.07	0.68		9
LUI × Social Status	Urban × Not obligately solitary	0.02	0.21	-0.01	0.22	-0.42	0.43		48
mNDVI × Lecty Status	mNDVI × No lecty status	-1.92	0.64	-0.02	0.65	-3.22	-0.71	*	-
mNDVI × Lecty Status	mNDVI × Not obligately oligolectic	-1.34	0.53	-0.01	0.54	-2.45	-0.28	*	-
LUI × Tongue length	Cropland (Minimal use) × Short tongue	0.26	0.16	-0.00	0.16	-0.05	0.59		93
LUI × Tongue length	Cropland (Light use) × Short tongue	0.36	0.15	-0.00	0.15	0.06	0.68	*	51

LUI × Tongue length	Cropland (Intense use) × Short tongue	0.35	0.15	-0.00	0.15	0.06	0.67	*	34
LUI × Tongue length	Pasture × Short tongue	0.52	0.16	0.00	0.16	0.22	0.86	*	36
LUI × Tongue length	Urban × Short tongue	0.32	0.18	-0.00	0.18	-0.03	0.67		99
mNDVI × Tongue length	mNDVI × Short tongue	-1.70	0.37	-0.01	0.35	-2.40	-1.03	*	-
LUI × Voltinism	Cropland (Minimal use) × Not obligately univoltine	0.13	0.18	-0.00	0.18	-0.21	0.47		69
LUI × Voltinism	Cropland (Light use) × Not obligately univoltine	0.13	0.17	-0.00	0.17	-0.21	0.45		19
LUI × Voltinism	Cropland (Intense use) × Not obligately univoltine	0.15	0.17	-0.00	0.16	-0.16	0.47		10
LUI × Voltinism	Pasture × Not obligately univoltine	-0.46	0.19	0.00	0.18	-0.81	-0.09	*	-49
LUI × Voltinism	Urban × Not obligately univoltine	-0.00	0.19	0.00	0.19	-0.37	0.37		44
LUI × Flight season duration	Cropland (Minimal use) × Flight season duration	-0.09	0.04	0.00	0.04	-0.16	-0.02	*	-
LUI × Flight season duration	Cropland (Light use) × Flight season duration	-0.04	0.04	0.00	0.04	-0.12	0.03		-
LUI × Flight season duration	Cropland (Intense use) × Flight season duration	-0.03	0.04	0.00	0.04	-0.10	0.04		-
LUI × Flight season duration	Pasture × Flight season duration	-0.01	0.04	0.00	0.04	-0.09	0.07		-
LUI × Flight season duration	Urban × Flight season duration	-0.08	0.05	0.00	0.05	-0.18	0.01		-
mNDVI × ITD	mNDVI × ITD	-0.41	0.12	-0.00	0.11	-0.64	-0.19	*	-

Table S4.3: Random effect variances ± one standard deviation.

Random effect	Occurrence	Abundance
Source ID	2.17 ± 1.47	1.38 ± 1.17
Study within source	0.57 ± 0.75	0.08 ± 0.28
Block in study in source	0.27 ± 0.52	0.01 ± 0.12
Family	0.16 ± 0.40	0.07 ± 0.27
Species within family	0.83 ± 0.91	0.12 ± 0.33

S4.1 Interactions between traits and mDNVI

Species with smaller ITD were significantly more sensitive to areas of low habitat quality (mNDVI) than those with larger ITD (Fig. S4.1). Species with narrow dietary breadths were more sensitive to habitat quality, responding significantly more positively to mNDVI than species that are polylectic (occurrence model estimate = -3.97, bCIs:-6.01,-3.74; abundance model estimate = -1.34, bCIs:-2.45, -0.28) or parasitic (occurrence model estimate = -4.86, bCIs:-5.14, -3.06; abundance model estimate, -1.92, bCIs:-3.22, -0.71). Similarly, long-tongues species were more sensitive to mNDVI than short-tonged species (occurrence model estimate = -1.71, bCIs:-1.44, -0.70; abundance model estimate = -1.70, bCIs:-2.40,-1.03). Social species were also more sensitive to decreasing mNDVI than solitary species (occurrence model estimate = 1.94, bCIs:0.80,2.87)

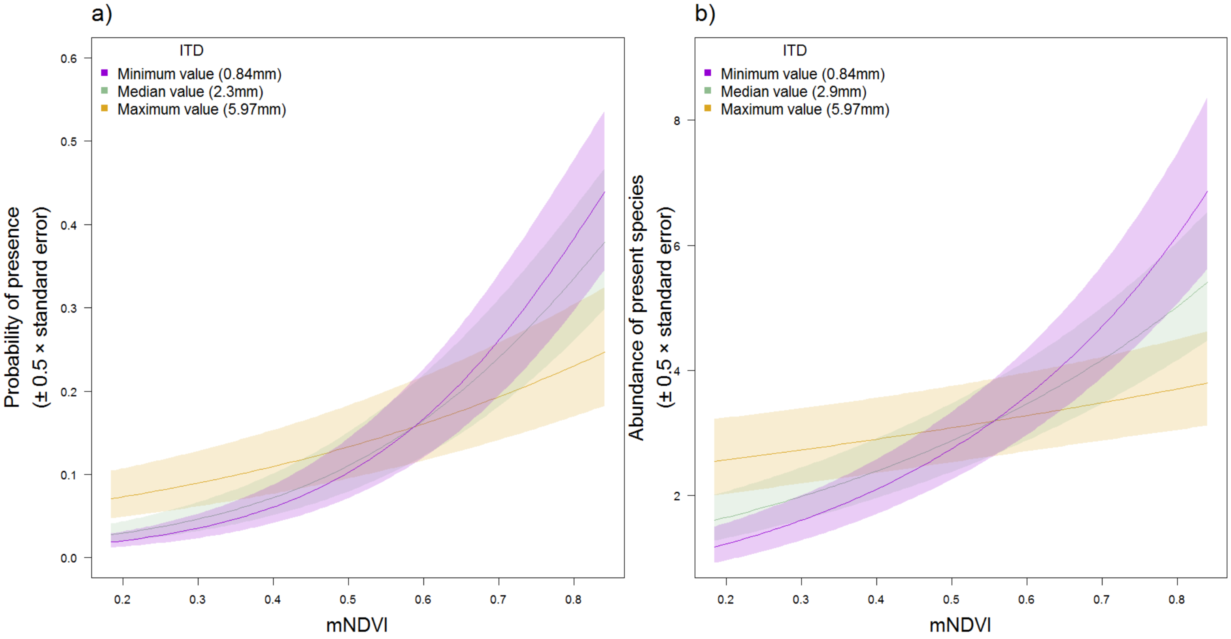


Figure S4.1: Relationship between mNDVI and a) probability of species presence and b) the abundance of present species, predicted for three different body sizes (minimum, median, and maximum ITD values observed in the original dataset). Error bars represent half the standard error (estimated from model coefficients), to ease comparison. The coefficient estimate of ITD × mNDVI was -0.67 (bootstrapped Confidence Intervals, bCIs: -0.96, -0.41) for the occurrence model; and -0.41 (bCIs: -0.64, -0.19) for the abundance model. Where bCIs do not cross zero, the coefficient estimate is taken to be significant.

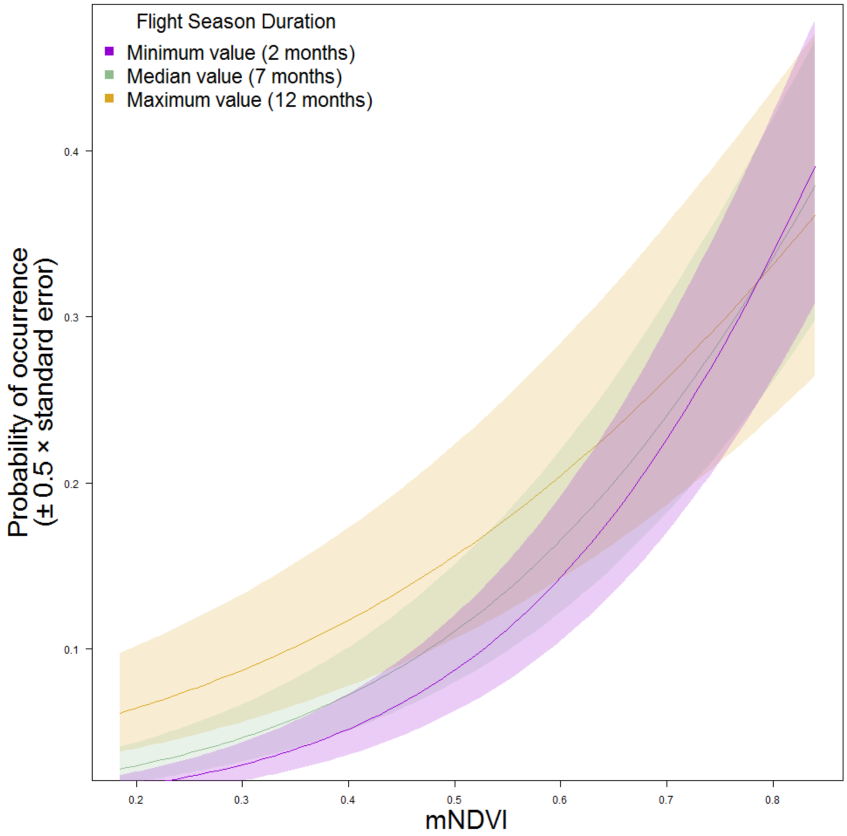


Figure S4.2: Relationship between the probability of species presence and mNDVI, at three different flight season durations (minimum, median, and maximum). Error bars represent half the standard error, to ease comparison between slopes. Coefficient estimate of flight season duration × mNDVI = -0.23 (95% bootstrapped confidence intervals, bCIs = -0.40 and -0.07). Note that where bCIs do not cross zero, the coefficient estimate is taken to be significant.

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Dear Miss Adriana De Palma,

Thank you for submitting your revised manuscript to the Journal of Applied Ecology. I have now received a recommendation from the Associate Editor who handled the review process. As you will see, they appreciate the effort you have put into the revision and remain positive about the value of the work although they have made a number of suggestions for further improvement. I have considered your paper in the light of the comments received and I would like to invite you to prepare a second revision. I would like to emphasize and add to the AEs point about the use of NDVI. I did not find your response to the reviewers very convincing - surely you need to test to what extent woodland is affecting NDVI, rather than just stating it is unlikely it has one. Was tree cover really only present in a few of the 1500 sites? Without a more refined approach, it is very hard to interpret what NDVI is telling us as it could be either reducing or increasing habitat quality for the focal taxa.

Following the suggestion of the associate editor, we have de-emphasised NDVI in the paper, and have moved all associated results into the appendix. We have restructured the methods section, so that NDVI is introduced as a continuous variable that may provide additional information over the discrete, fairly coarse land use and intensity measure (see lines 120-122):

"As well as using a coarse, discrete variable of land use, we also used remotely-sensed mean Normalized Difference Vegetation Index (NDVI), to capture additional variation in vegetation between sites."

An analysis of influence revealed that those sources where woodland is known to be present do not overly influence the model results, suggesting that wooded sites are not having a strong effect on the results. We have included this in the revised text (See Lines 131-133):

"wooded sites were only present in two of 24 sources (three sites in woodland and two in mixed woodland/agriculture) and these sources were not particularly influential (as judged by Cooks distance values; all <= 0.097)."

Furthermore, links between NDVI and species richness are obviously both ecosystem and scale dependent - is there any evidence that NDVI is a strong predictor of plant richness in 250m buffers, or any alternative validation of the use of this metric? Citations from 25ha grid squares in northern Finland are not useful in this instance, as that particular study analysed gradients from closed canopy forests to open mires and cannot be used to support your claim about habitat quality for pollinators.

As stated above, we now present the results for mNDVI in the supplementary material. However, we also now include references for studies that have used NDVI at smaller spatial scales (lines 122-124):

"NDVI is highly correlated with above-ground biomass and net primary productivity (Pettorelli et al. 2005), and often correlates positively with plant and invertebrate species richness even at relatively small spatial scales (e.g. Gould 2000; Lassau & Hochuli 2008)."

New Reference:
Lassau, S.A. & Hochuli, D.F. (2008) Testing predictions of beetle community patterns derived empirically using remote sensing. Diversity and Distributions, 14, 138-147.

I would be grateful if you would consider the above comments and those made in the reports below, and revise the paper again to take account of the salient points. Please note that Journal of Applied Ecology does not automatically accept papers after revision, and an invitation to revise a manuscript does not represent commitment to eventual publication on our part. We will reject revised manuscripts if they are overlength, insufficiently focussed or returned without satisfactory responses to the referees' comments. When returning the revised paper, please show point-by-point how you have dealt with the various comments in the appropriate section of the submission form. Ensure that you upload a Word version of the paper as we may need this for editing (see Instructions below).

Your revision must be received within three weeks of the date of this message unless a later date has been agreed with us. Manuscripts received after this time may be treated as new submissions and subjected to further review, or even rejected outright. Please let me know if this schedule is likely to prove difficult.

We look forward to hearing from you in due course.

Yours sincerely,

Dr Jos Barlow
Editor
Journal of Applied Ecology

COMMENTS FROM ASSOCIATE EDITOR: Dr Ian Kaplan

Associate Editor
Comments to the Author:
I felt that the authors did a good job in their revision of addressing the reviewers' concerns from the original submission. Although the paper is an improvement, there are still aspects of the data presentation that are difficult to follow. Unfortunately some of this may simply be a feature that's inherent to this paper and its complex design, so I'm trying to be sensitive to this aspect while offering suggestions to improve its readability. Anytime you throw this many predictor variables and interactions into multiple responses it will be challenging for reviewers to follow along.

One option to simplify would be to either remove the mNDVI component or move all information associated with it into the appendix. You never show the mNDVI interactions, except for Figure 3. Also, what is the relationship between LUI and mNDVI? You may have mentioned this somewhere in the paper, but I never recall coming across this. I assume LUI affects mNDVI? Or at least that's how the mNDVI was set-up in the methods, as a proxy for habitat quality that's separate from LUI. I guess in the end I don't really know what I got from the mNDVI part so it seems like you either need to use it more or get rid of it.

Thank you for your suggestion. We have moved the majority of information pertaining to mNDVI into the appendix, except for an explanation of its inclusion in the models in the methods section and a brief mention in the results.

Line 239-241:

"Interactions between LUI and traits were more important than interactions between mNDVI and traits (Fig. 1); we therefore focus on the former in the main text (see Supporting Information S4.1 for full mNDVI results)."

As mentioned in detail above, we have restructured the methods section, so that NDVI is introduced as a continuous variable that may provide additional information over the discrete, fairly coarse land use and intensity measure (see lines 120-122).

The only other simplifying option would be to choose either abundance or occurrence to report, since you use both measures, but this difference seems important. Along those lines, I was surprised that land use seems to negatively affect species when quantified in terms of occurrence probability (Fig. 4), but in most cases positively affected species for abundance (Fig. 5). You wouldn't expect occurrence and abundance to be perfectly correlated, but I would think these two responses would be related and not show opposite patterns. Can you comment on this?

We agree that in general, species occurrence and species abundance are often correlated. However, in this case, we are looking at species occurrence and the abundance if present. In this case, you wouldn't necessarily expect to see similar responses. A decrease in the number of species (lower probability of presence), may enable remaining species to persist at higher abundances (higher abundance if present), for instance.

We have clarified this in line 216-218:

"Effects of trait × land use interactions were often different for species occurrence and abundance. A decrease in the number of species might enable remaining species to persist at higher abundances (Newbold *et al* 2014)."

Figure 2 needs to be either removed or majorly revised. My vision is pretty decent I cannot make out the differences between these color treatments.

We have used a bolder colour scheme and increased the width of the lines, to ease comparison between slopes. We agree that figures with many slopes are often hard to visualise, but have included the figure in light of comments from the initial review.

Figure 3. Can you clarify how you present these data? What you're calling the 'minimum' and 'maximum' value – is this just one species for each category? This is a strange way to graph these data, as opposed to say breaking your full dataset into thirds and graphing 'small' 'medium' and 'large' species.

This figure is no longer presented in the main paper as the majority of information pertaining to mNDVI is now shown in the appendix. Apologies that it was unclear: the relationships plotted are predicted from model coefficients, rather than showing the underlying data. In the appendix, we have amended the figure legend to clarify:

"Relationship between mNDVI and a) probability of species presence and b) the abundance of present species, predicted for three different body sizes (minimum, median, and maximum ITD values observed in the original dataset). Error bars represent half the standard error (estimated from model coefficients), to ease comparison. The coefficient estimate of ITD $\times$ mNDVI was -0.67

(bootstrapped Confidence Intervals, bCIs: -0.96, -0.41) for the occurrence model; and -0.41 (bCIs: -0.64, -0.19) for the abundance model. Where bCIs do not cross zero, the coefficient estimate is taken to be significant."

Figures 4 and 5. I'm not sure that I agree with how you approached these figures in grouping a whole category as 'Reference traits' and then separating out one level of each of the other factors. I've never seen this approach before and it's less than ideal because you're making it impossible to actually compare within a level for a specific factor. Ideally they'd be paired bars or data points on the same figure, i.e., short and long tongued both on the same figure.

We agree that paired plots would in principle be an effective way to compare levels within a factor. However, within each pair of plots, the first would be a repetition: the plots for long-tongued species would be identical to those for social species and oligolectic and univoltine and excavating species, as these are the reference levels within the model. In light of this, we have altered the figure to use the phrase 'reference levels' rather than 'reference traits' and have amended the figure legend to clarify how the figures should be read.

"Land use and intensity (LUI) impact on species with differing (categorical) ecological traits. For each trait level, this is shown as the % difference in probability of occurrence relative to secondary vegetation, with 95% confidence intervals (CIs) calculated from the model. The trait reference levels in the models were oligolectic, solitary, univoltine, long-tongued, and nest excavating species. The effect of LUI on species with these trait values is presented in panel a, and the effects on species with other trait values in panels b-g. Therefore, to compare the sensitivity of long-tongued species and short-tongued species to LUI, one would compare panels a and e. CIs in some panels extend beyond the plot region."

Minor points:
L65. Can you explain more about this Williams dataset and how it differs from yours (since you highlight it as the most similar)? Are you using the same studies in your reviews, only yours is a subset for Europe? Or are they totally separate datsets? Also, I'm surprised this paper didn't come up again in the Discussion as a comparison with how their results compare with yours.

Our dataset is different from the William's dataset. We have included a note in the introduction, differentiating our study from that of Williams et al's study:

"Unlike the study by Williams *et al* (2010), we analyse multiple traits within the same model." (Line 76-77)

We have also included more on this paper in the discussion section:

"Although our analyses are based on different datasets, these results are similar to those in Williams *et al* (2010) which found that social species and pollen specialists were particularly sensitive to agricultural intensification." (Lines 285-287)

L71. I don't understand this argument. Why are social bees more vulnerable to pesticides than solitary bees?

The argument here was more about how the same trait could potentially correlated with enhanced sensitivity in one land-use class, but not in another. This sentence has been clarified (Line 70-74):

"For instance, social species may be more sensitive in intensively-used cropland—where enhanced foraging capacity can increase exposure to pesticides and thus affect mortality and colony success—but relatively less sensitive in urban areas, where greater foraging capacities may enable persistence."

In addition, we have clarified table 1:

"Enhanced foraging capacity may also increase pesticide exposure (as foragers using various resources in different areas may bring pesticide-containing pollen and nectar back to the nest, Brittain & Potts 2011)"

L80. Can you cut the 2nd part of this sentence (everything after "land use")? It's just strange to set up a concrete prediction in the first part of the sentence and then undercut this with vague uncertainty in the latter half. If you have specific ideas about how land use impacts species with various traits then introduce this as a separate hypothesis. However, saying that your predictions won't work 100% of the time is not helpful.

We have removed the end of the sentence as suggested, which now reads as (line 80-82): "We hypothesize that resource and phenological niche breadth, foraging range and reproductive strategy will all influence species' sensitivity to land use."

L104. Can you comment more on the purpose of these studies you were using? Were there treatments imposed within these studies or were they purely sampling designs? If there were experimental manipulations, did you just use the control data?

We have included more detail in the manuscript as suggested (line 105-108):

"In all but one case, this was the sampling design of an observational study. Only one study included was an experimental project, where only the control data were extracted; this study had extremely low influence on the final models (based on Cook's distance, influence.ME package, Niewenhuis, te Grotenhuis & Pelzer 2012) and did not qualitatively change the results."

L280-281. You state here that polylectic species were the only ones unaffected by intense cropland. I don't follow this. In Fig. 4d, polylectic species show a sharp decline from minimal to light to intense like the others. Is this a mistake or am I interpreting this statement incorrectly?

This statement has been clarified (line 275-277) as although there was a decline in diversity as cropland intensity increased, the probability of presence did not differ strongly to that in secondary vegetation:

"The probability of presence for most species was strongly reduced in intensively-used cropland relative to secondary vegetation, except for pollen generalists (polylectic, flexible or parasitic species)"

I’m glad you mentioned that factors such as flight season duration affect the probability of sampling as a limitation, especially since this was such an important factor (according to Fig. 1). However, I’m not sure I understood your explanation of how mNDVI affects the likelihood of capture (L336-337). Can you clarify?

Thank you for your comment. The idea is that where sampling is based on visual observation (aerial transect for example), one would expect to see more small species where the vegetation is less dense, and fewer small species where the vegetation is denser (as small species are harder to spot in denser vegetation), making this result likely to be conservative if anything. This is the opposite of what we find (more small species in denser vegetation – high mNDVI areas). However, this only holds for studies where sampling is on a visual basis, rather than pan traps for instance.

We have clarified this in the text (Line 326-334):

“Some effects may be influenced by differential detectability; for instance, larger species that are active for longer are more likely to be sampled. This is in part why we have focussed on differences in sensitivity—changes between secondary vegetation and human-dominated land uses—rather than absolute differences in occurrence and abundance between species. However, detectability may vary among land uses. For instance, with visual sampling methods such as aerial transects, small species may be less frequently sampled in denser vegetation where they are more difficult to see. This may be in part accounted for by the inclusion of mNDVI in our models (as NDVI correlates with net primary productivity), but it is still important to consider possible effects of sampling bias on analyses such as these.”