

## Research

### On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution

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The response and effect trait framework, if supported empirically, would provide for powerful and general predictions about how biodiversity loss leads to loss in ecosystem function. This framework proposes that species traits will explain how different species respond to disturbance (i.e. response traits) as well as their contribution to ecosystem function (i.e. effect traits). However, predictive response and effect traits remain elusive for most systems. Here, we use data on crop pollination services provided by native, wild bees to explore the role of six commonly used species traits in determining both species' response to land-use change and the subsequent effect on crop pollination. Analyses were conducted in parallel for three crop systems (watermelon, cranberry, and blueberry) located within the same geographical region (mid-Atlantic USA). Bee species traits did not strongly predict species' response to land-use change, and the few traits that were weakly predictive were not consistent across crops. Similarly, no trait predicted species' overall functional contribution in any of the three crop systems, although body size was a good predictor of per capita efficiency in two systems. Overall we were unable to make generalizable predictions regarding species responses to land-use change and its effect on the delivery of crop pollination services. Pollinator traits may be useful for understanding ecological processes in some systems, but thus far the promise of traits-based ecology has yet to be fulfilled for pollination ecology.

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#### Introduction

Land-use change, along with other human-induced global change drivers, is accelerating the rates of extinction of most taxa (Ellis et al. 2010). At the same time, humanity relies on ecosystem services that wild species deliver, such as pollination and pest control by insects, and nutrient cycling by microorganisms (Cardinale et al. 2012). Thus, it is important to understand the relationship between biodiversity loss and ecosystem service delivery (Schwartz et al. 2000). In particular, making generalizable predictions regarding how the decline or local extinction of taxa will affect ecosystem services will allow for targeted conservation actions to ameliorate negative impacts of land-use change.

One avenue for predicting the functional consequences of biodiversity loss is the response and effect trait framework (Lavorel and Garnier 2002, Naeem and Wright 2003, McGill et al. 2006). Local extinction does not occur at random because extinction risk is dependent on the species' characteristics. Identifying which traits govern species responses to particular threats ('response traits') would provide the first step for predicting future species loss. Furthermore, the magnitude by which ecosystem function declines when a species is lost depends on that species' functional contribution. This, too, is likely to be mediated by the species' traits ('effect traits'). Therefore, the relationship between response and effect traits will mediate the magnitude of the impact of human disturbance on ecosystem services (Schleuning et al. 2015). For example, if the same species traits that are associated with high function are also most sensitive to disturbance, ecosystem function would be predicted to decline rapidly (Larsen et al. 2005).

However, for the response-effect trait framework to be useful, it is first necessary to identify response and effect traits that are both explanatory and possible to measure in the field or in the lab (Cadotte et al. 2011). While a few candidate traits have emerged to predict which animal species are at greater risk of local decline, including dietary or habitat specialization and body size (Fisher and Owens 2004, Flynn et al. 2009, Öckinger et al. 2010), the correlation between these response traits and species population declines has been found to be weak, variable, and often context-dependent (Devictor et al. 2008, Fritz et al. 2009, Powney et al. 2014). Similarly, although some effect traits have been identified, they are often weakly predictive, and their identity varies by function and taxonomic group (Gagic et al. 2015). Lastly, within the functional trait field as a whole, most progress has been made in identifying functional traits for plants (Díaz et al. 2016), while comparatively little is known for animals (Didham et al. 2016).

Here, we seek to test simultaneously the strength of both response and effect traits for wild bee species providing a key ecosystem service, crop pollination. The yield of most crop plants increases with animal pollination (Klein et al. 2007). While managed honey bees are a leading crop pollinator, wild insects contribute more than half of pollinator visits to crop flowers across more than 40 crop systems worldwide (Rader et al. 2016). Conversion of natural and semi-natural habitats to agriculture can reduce pollinator populations (Garibaldi et al. 2011); thus agricultural land use affects one of the ecosystem services upon which agriculture itself depends (Deguines et al. 2014). However, not all pollinators are equally affected by land-use change, and some species show positive responses to agricultural land use. Thus there is an expectation that ecological traits may explain those differential responses, as well as the extent to which pollination services are resistant to land use change.

Our data sets were collected and analyzed in parallel and come from three crop systems (watermelon, cranberry and blueberry) located within the same geographical region (mid-Atlantic USA), but pollinated by distinct bee communities.

We determined whether six commonly-used species traits can predict 1) species' responses to land-use change (response traits) and/or 2) species' contributions to crop pollination (effect traits). In contrast to many previous studies of pollination, we measure both response and effect traits within the same systems and discuss our results in the light of recently published studies on pollinator-environment-trait and pollination-trait associations.

## Material and methods

### Study system

We selected 49 sites across three crop systems that were located throughout New Jersey and eastern Pennsylvania (USA). Watermelon sites ( $n = 17$ ) were located in a  $90 \times 60$  km region in central New Jersey and eastern Pennsylvania, where the main types of land use are agriculture and suburban development, interspersed with highly fragmented deciduous forest. Cranberry and blueberry sites ( $n = 16$  each) were both located within a  $35 \times 55$  km area in southern New Jersey, where the main land-cover types are pine-oak ericaceous heath and agriculture. All sites in all systems were separated by at least 1 km (range, watermelon: 2–90 km, cranberry: 1–32 km, blueberry 1–38 km).

All three crops are highly dependent upon bee pollination for marketable fruit production (Klein et al. 2007). Commercial honey bees are used in most of our study fields. However, honey bees are primarily managed hives, moved throughout the region, and only found on sites during bloom. Therefore, honey bees are not influenced by land cover in the same manner as wild bees and are not used in our analyses. Wild bees are important pollinators in all three systems (mean percentage of wild bee visits: 73% watermelon, 25% cranberry, and 14% blueberry).

### Data collection

At all sites on all three crops, we used hand-netting to measure overall bee abundance. To collect bees we walked along fixed transects during both the morning and the afternoon, and collected all bees observed to be visiting flowers. Transects ranged between 60 m (cranberry) and 200 m (blueberry). In watermelon and blueberry, bees were netted three times throughout the day for 20 min per transect (60 min per date per site) and twice each day in cranberry for 30 min per transect (120 min per date per site). Data were collected during the peak bloom in 2010 (watermelon: July, cranberry: late-May-early July, blueberry: April-early May). Data were collected on three days per site for watermelon and blueberry and two days per site for cranberry. We met with extension agents that worked with these growers and selected farms that had similar management practices for each crop. All blueberry and cranberry farms were conventionally managed but with similar and reduced pesticide inputs based on IPM (integrated pest

management). Watermelon farms included both conventional and organic, but were all small, family-owned operations for which conventional management involved limited pesticide use based on IPM. Detailed methods can be found in Cariveau et al. (2013), Benjamin et al. (2014) and Winfree et al. (2015).

### Land-cover characteristics of sites

To relate pollinator response traits to land-use change we used a commonly used land-use variable, percent of relevant categories of land cover surrounding a site (Fahrig 2013). For this end, we required high-quality land cover data for each site. For the cranberry and blueberry sites in New Jersey, we used a continuous polygon layer classified by visual photograph interpretation into 60 categories, at a minimum mapping unit of 4047 m<sup>2</sup> (1 acre; NJDEP 2007). For watermelon sites that extend from central New Jersey into Pennsylvania, we created a similar land cover data layer by manually digitizing Google Earth imagery from 2010 and visually classifying 15 categories, at a minimum mapping unit of 5000 m<sup>2</sup> (1.24 acres). As each crop was analyzed separately, our results are robust to using different land cover data. However, to simplify the interpretation of results for the three crops, we reclassified all land cover data into the following seven broad categories: agriculture, open managed (for example, mowed grass), open natural or semi-natural (for example, old fields), semi-urban (< 30% impervious surface), urban (> 30% impervious surface), wooded and open water.

For each data collection site, we calculated two uncorrelated land cover variables: percent agriculture and percent natural and semi-natural open habitat (hereafter 'open semi-natural habitat'). We used agricultural land cover as our primary land-use change variable as it is the dominant anthropogenic habitat type in all three study systems (Supplementary material Appendix 1 Table A1). We measured percent of open semi-natural habitat, which although it accounts for only a small proportion of the total land cover (Supplementary material Appendix 1 Table A1), might be disproportionately important as forage and nesting habitat for bees (Kleijn et al. 2006). We calculated values for these two land cover variables at both a small scale (300 m radius) and a large scale (1500 m radius), which correspond to typical flight distances of small- and large-bodied bees, respectively (Greenleaf et al. 2007). See Supplementary material Appendix 1 Fig. A1 for correlation among land-use variables and Supplementary material Appendix 1 Fig. A2 for an analysis of confounding environmental variables like forest edges, which can potentially influence nesting site availability.

### Pollinator function

To estimate the pollination services provided per bee species, we measured two variables in the field, flower visitation frequency and per visit efficiency. As variation in visitation frequency may be a function of land-use change at individual farms, we use species visitation frequency for

each species at the site with its highest visitation frequency for each crop. Hence, we assess visitation frequency at its maximum.

To measure the pollination efficiency, we quantified single-visit pollen deposition by presenting virgin flowers to individual bees foraging on the target crop. After visitation, we counted the number of pollen grains deposited per flower visit (watermelon) or the number of pollen tetrads with pollen tubes per flower visit (cranberry and blueberry). Because species identification in the field is not possible for most bees and net collecting immediately after visits was generally not possible for this study, for the measurement of pollination efficiency we grouped bees in species groups. Each group consisted of functionally similar species in terms of size, color and pollen carrying structures and ranged between one and 27 species, with the median number of species per group being 4 species (Supplementary material Appendix 1 Table A2). Control flowers were left bagged until the end of the field day, and contained few pollen grains (watermelon mean = 3 grains, n = 40 stigmas; cranberry mean = 0 tetrads, n = 82 stigmas; blueberry mean = 2 tetrads, n = 734 stigmas). We used mean number of pollen grains deposited by a single species group and assigned that value to each of the species in the species group. For detailed methods see Cariveau et al. (2013), Benjamin et al. (2014), Winfree et al. (2015).

### Species traits

Bee species vary in a number of traits that are associated with their response to land-use change (Williams et al. 2010). Moreover, these traits will likely affect the pollinator contribution to function, either by modifying its abundance or because they are related to its per capita effectiveness. We obtained detailed natural history data on six traits for the 90 bee species in our study: 1) sociality (solitary, facultative social, eusocial), 2) nesting placement (pre-existing holes in wood, large cavities, stems, decaying wood, ground), 3) brood parasite (yes, no), 4) body size, 5) diet breadth (level of generalism) and 6) tongue length. All parasites were considered solitary. We categorized nest placement of parasites based on the host nesting placement. Floral diet breadth of parasites was calculated using the same methodology as other species explained below.

We obtained the trait data as follows. Species sociality level, nesting placement and brood parasite status were extracted from the literature (Bartomeus et al. 2013a). Body size (estimated from intertegular span, IT; Cane 1987) was measured in the lab using a variety of collected specimens from the region that had been identified to the species level by professional taxonomists. Multiple female specimens were measured per species (mean = 6.6 specimens  $\pm$  3 SE) and the mean across the measured specimens was used as the value for the species. Bee body size also correlates strongly with foraging distance (Greenleaf et al. 2007), and thus is ecologically related to mobility. Tongue length was measured in the lab for 7.7  $\pm$  1.2 SE specimens per species, and the mean across

the measured specimens is used (see details in Cariveau et al. 2016). For the 40 species for which we could not directly measure tongue length, we estimated tongue length from the species' body size and taxonomic family using an allometric equation (Cariveau et al. 2016).

Diet breadth was calculated using six independent datasets previously collected at 139 sites throughout the study region by the Winfree laboratory group. Each data set consists of individual pollinator specimens that were net-collected while foraging on a flowering plant species; both pollinator and plant were then identified to the species level. Those datasets comprise overall 393 pollinator species, and 392 plant species, with 3890 plant–pollinator interactions (Supplementary material Appendix 1 Text A1). Prior to calculating diet breadth, we rarefied the data to 20 visitation records per bee species, to avoid confounding rarity with specialization (Blüthgen et al. 2008, Winfree et al. 2014). Nine species had fewer than 20 records and we were unable to estimate diet breadth in the manner described above. Of these species, five are known to be specialized on one or two plant species. For these species, we calculated the diet breadth index corresponding to 20 individuals visiting the known host plants in equal proportions. The four other species are known generalists and we therefore used the mean diet breadth of their genus. These four species were extremely rare (< 5 records each) in our analyzed dataset.

To calculate diet breadth for each bee species, we considered the number of plant species as well as the phylogenetic breadth that the bees fed upon by using a rarefied phylogenetic diversity index (Nipperess and Matzen 2013). To determine phylogenetic distances among plants, we first constructed a general phylogenetic tree using the PHYLOMATIC 'megatree' (ver. R201120829, Chamberlain and Szöcs 2013) which defines relationships among higher plants (Webb et al. 2008). We then dated nodes across this tree according to Wikström et al. (2001) and used the branch-length adjustment algorithm BLADJ to estimate the age of all remaining, undated nodes. Though this procedure implies that ages within our phylogenies should be treated as approximations (Beaulieu et al. 2007), previous analysis indicates marked improvements of phylogenetic analyses when even a limited number of nodes are properly dated (Webb 2000). For comparison with other studies, we also present all results for a categorical diet breadth variable extracted from the literature, which classifies bees as oligolectic or polylectic (Supplementary material Appendix 1 Fig. A3). Correlations among traits can be found in Supplementary material Appendix 1 Fig. A4.

## Statistical analysis

### Response traits

To investigate which traits are associated with environmental variables related to land-use change (i.e. the proportions of two key habitat covers at two different scales), we used a model-based approach to the fourth-corner problem (Brown

et al. 2014). The fourth-corner problem highlights the difficulty of studying environment–trait associations and can be conceptualized as a set of four matrices: abundances by species, trait data by species, environmental data by sites, and environmental data by traits, with the relationships of this last corner being the ones to be estimated (Legendre et al. 1997). The core idea of the model-based approach is to fit a predictive model for species abundance as a function of environmental variables, species traits and their interaction. The environment–trait interaction coefficients can be understood as the fourth corner and describe how environmental response across taxa varies as traits vary. The size of coefficients are a measure of importance, and are interpreted as the amount by which a unit (1 SD) change in the trait variable changes the slope of the relationship between abundance and a given environmental variable. To estimate these coefficients, we used a LASSO-penalised negative binomial regression (R package 'mvabund', Wang et al. 2012). The LASSO penalty aids in interpretation as it completes model selection by setting to zero interaction coefficients that do not reduce BIC (Wang et al. 2012). A species effect is included in the model (i.e. a different intercept term for each species), so that traits are used to explain patterns in relative abundance across taxa, not patterns in absolute abundance. Pseudo- $R^2$  is calculated as the  $R^2$  of the predicted against the observed abundance values for each species at each site. Each crop was analyzed separately.

### Effect trait analysis

To determine which traits influenced the functional contribution of each species, we ran separate linear models with either visitation or per capita efficiency as response variables. Species traits were predictors. The best model based on AICc was selected. When differences between the best models were less than 2 we selected the simpler model. Variance inflation factors (VIF) were calculated on this model to avoid collinearity problems. When VIF were > 2, we removed the problematic variable, and discuss the implications. The analysis for efficiency was done at the species group level (see above: Pollinator function section). To obtain traits at the species-group level, we calculated for each system the mean values over species belonging to the same group, weighted by the species mean abundance within the group. For categorical variables we chose the dominant level, again weighted by species abundance. This way, we assure that while species within a functional group are selected to be functionally similar, the average trait used reflects species composition.

All residuals were visually inspected to validate model assumptions. All statistical analyses were performed in R (ver. 3.0.3 <[www.r-project.org](http://www.r-project.org)>).

### Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.716kr>> (Bartomeus et al. 2017).

All data and code used in this manuscript is accessible in github (<[https://github.com/ibartomeus/RE\\_traits](https://github.com/ibartomeus/RE_traits)>).

## Results

We collected 1961, 1761 and 233 specimens belonging to 45, 41 and 22 species in watermelon, cranberry and blueberry respectively.

### Response traits

Overall, we did not find a strong correlation between any ecological traits and the environmental variables analyzed, despite finding that the aggregate abundance of bees did change with land-use variables (watermelon: coefficients for the percentage open semi-natural habitat at 300 m = 0.12; blueberry: coefficients for the percentage agricultural

habitat at 300 m = -0.26 and at 1500 m = -0.12; cranberry: coefficients for the percentage agricultural habitat at 1500 m = -0.23. Numbers represent model coefficients, see methods for details on interpretation; see Supplementary material Appendix 1 Table A3 for all regression coefficients). Traits did not modify these slopes in most instances, and although some traits exhibited weak responses to land use in some cases, these responses were not consistent across crops (Fig. 1). For watermelon (overall pseudo- $R^2 = 0.54$ ), small bees and parasites tended to decline with increasing percentage of agriculture at 300 m radius (interaction coefficient of % agriculture at 300 m with body size = 0.19, Fig. 1D; and with parasitism = 0.10) and parasites also declined with increasing open semi-natural areas at 1500 m radius (interaction coefficient = 0.13). In cranberry (overall pseudo- $R^2 = 0.59$ ), bees nesting in wood and generalist bees tended to increase with increasing open semi-natural areas at 300 m (interaction coefficient = 0.14 and 0.11 respectively)

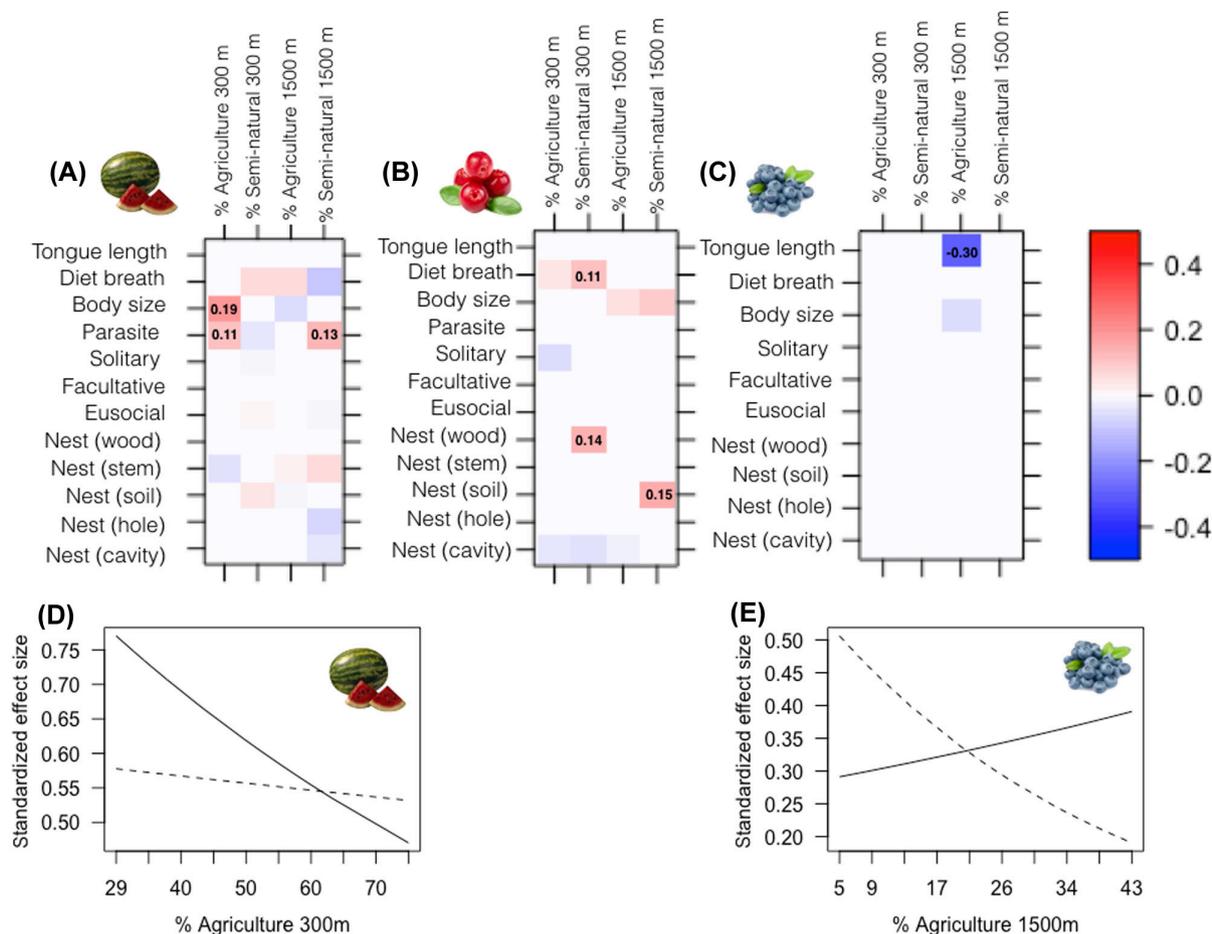


Figure 1. Relationships between traits and environmental variables for (A) watermelon, (B) blueberry and (C) cranberry. Positive estimates are in red and negative estimates in blue. The larger estimates are shown in bold. Note that the LASSO penalty has set many estimates to zero. Detail of the mean predictions from the model for two of the stronger interactions between (D) body size and percentage of agriculture at 300 m radii for watermelon and (E) tongue length and percentage of agriculture at 1500 m radii for blueberry. The solid line is the prediction for the 25 percentile of body size and tongue length, while the dashed line is the prediction for the 75% of body size and tongue length for watermelon and blueberry respectively. Note that these predicted lines are useful for showing the trends, but that the correlation values are still low.

and bees nesting in soil and bigger bees tend to increase with increasing open semi-natural areas at 1500 m buffer (interaction coefficient = 0.14). For blueberry (overall pseudo- $R^2 = 0.22$ ) short-tongued species increased with increasing agriculture at 1500 m (interaction coefficient = -0.30, Fig 1E). A complete list of all comparisons is presented in Supplementary material Appendix 1 Table A3).

### Effect traits

As for response traits, no traits were highly predictive of either of our effect traits, visitation frequency or per visit efficiency. For watermelon, the best model for visitation frequency does not include any trait. However, per visit efficiency was positively correlated with body size and tongue length. These two variables are highly correlated ( $VIF > 4$ ) and to avoid collinearity problems we present just the model with body size ( $R^2 = 0.75$ ,  $F_{2,9} = 17.07$ ,  $p < 0.001$ , Fig. 2A). In cranberry, cavity nesters tend to show higher visitation frequencies ( $R^2 = 0.38$ ,  $F_{4,36} = 7.1$ ,  $p < 0.0001$ , Fig. 2B). This result was driven by *Bombus* species, which are the only cavity nesters in this data set. In cranberry per visit efficiency was not related to any trait. For blueberry, efficiency per visit was positively related to tongue length ( $R^2 = 0.70$ ,  $F_{1,5} = 14.9$ ,  $p = 0.01$ , Fig. 2C), while visitation frequency was negatively related to diet breadth ( $R^2 = 0.37$ ,  $F_{1,20} = 13.5$ ,  $p = 0.001$ , Fig. 2D). An overview of best models (AICc  $\leq 2$ ) for each response variable and crop systems is given in Supplementary material Appendix 1 Table A4.

### Discussion

Identifying traits that characterize which species are more sensitive to land-use change or those that are functionally important is complex. We found some evidence for response and effect traits but they differed among crop species and also varied with the landscape variable used. Therefore, while some traits may be important in some contexts, no traits were generalizable enough to be used to predict how land-use change will influence the delivery of pollination. Further, the relationships identified were weak. This does not negate the importance of traits for understanding which mechanisms underlie species responses to land-use change and in turn pollination effectiveness, but it does suggest that traits commonly used for wild bees have not yet achieved this goal. In fact, the trait-based literature in general is characterized by mostly weak and/or idiosyncratic relationships between traits and either species responses or functional effects (Williams et al. 2010, Bartomeus et al. 2013b, De Palma et al. 2015, Carrié et al. 2017).

Being able to identify strong response traits would be a key tool for understanding extinction risk, and an asset for conservation planning. However, characterizing extinction risk based on traits is challenging. Despite some generalities that emerge across taxa, with rare species, big species, specialists, and higher trophic levels being in general more sensitive to disturbances (Fisher and Owens 2004), there is a large variation in the response of the species with those traits (Fritz et al. 2009, Séguin et al. 2014). Work specifically on native bees has found that traits such as specialization, body size, and sociality may predict responses to land use

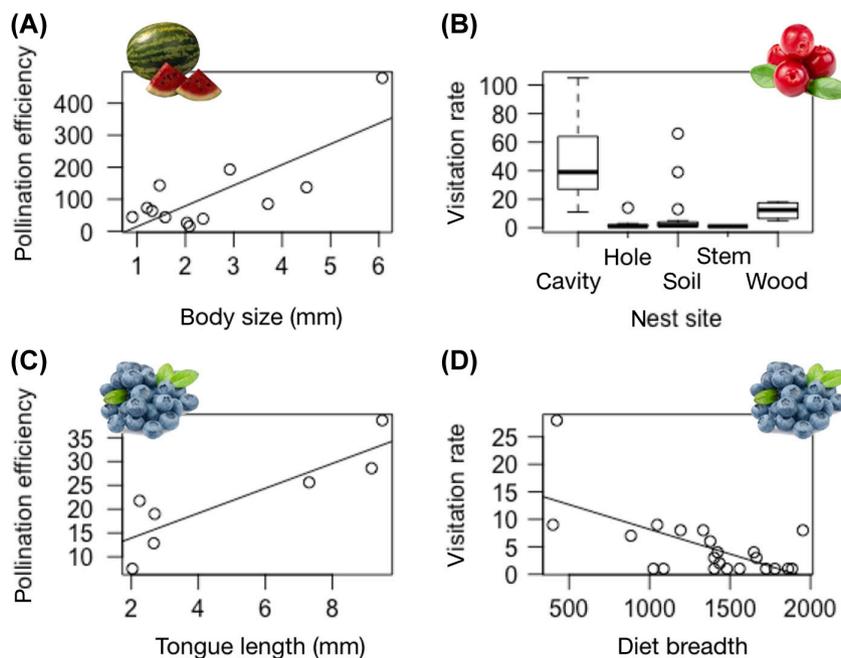


Figure 2. Relationships between species traits and pollination function, which is decomposed into efficiency (pollen deposited per flower visit) and frequency of flower visits (visits per transect). (A) watermelon, (B) cranberry, (C–D) blueberry. Note that high dietary breadth values (sample size corrected phylogenetic distance of known plants visited) imply that a species is more generalist.

(Winfree et al. 2009, Bommarco et al. 2010, Williams et al. 2010, Bartomeus et al. 2013b, Hopfenmüller et al. 2014, Rader et al. 2014, De Palma et al. 2015, Kremen and M'Gonigle 2015, Carrié et al. 2017). However, studies often find contrasting results. For example, De Palma et al. (2015) analyzed over 70 000 wild bee records and found that small species were most sensitive to agricultural land use, while others have found that larger species are more sensitive to agricultural land use and/or environmental change generally (Larsen et al. 2005, Bartomeus et al. 2013b), and some have found little effect of body size (Williams et al. 2010, Forrest et al. 2015). Here, we found a weak trend for small species to be more sensitive to local land-use change in watermelon, but this trend disappears when land use is measured at larger scales. Another trait, dietary specialization, is one of the few traits that has been generally linked to increased species sensitivity to environmental change (Williams et al. 2010, Scheper et al. 2014, De Palma et al. 2015), but here we found that floral specialist bees did not decline with intensifying agriculture. In fact, one of the most abundant bee species in the cranberry system *Melitta americana* is a specialist on cranberry *Vaccinium macrocarpon* (Cariveau et al. 2013). Specialist bees observed in crop systems are likely to be specialized on the crop plant family, as was the case in our data (e.g. *Melitta americana* in cranberry, but also *Habropoda* sp. and *Andrena bradleyi* in blueberry and *Peponapis pruinosa* in watermelon). Other studies have also found that specialist bees persist well in anthropogenic habitats provided that their host plant species does also (Hinners et al. 2012, Forrest et al. 2015).

Alternatively, the lack of strong trait–environment associations may be due to the variables used to measure land-use change being too coarse to detect common responses (but see Supplementary material Appendix 1 Fig. A2 for finer scale analysis on forest edges, which was also not predictive). While finer-resolution studies will undoubtedly be informative, they are unlikely to lead to a greater likelihood of predicting how changes in biodiversity affect the delivery of ecosystem services, if these smaller-scale environmental measures are difficult to quantify or are context-dependent.

Effect traits have been even harder to identify for pollinators than response traits. The limited data published on particular plants suggests insects with larger bodies tend to deposit more pollen per flower visit, but this pollen may not be well distributed on the stigma (as inferred from bee movements; Hoehn et al. 2008), and the correlation between body size and per-visit pollination function is low (Larsen et al. 2005). Our study supports the positive correlation between body size and per-visit pollen deposition in both watermelon and blueberry (although note that bee tongue length is correlated with bee body size for the blueberry system:  $r = 0.76$ ), but not for cranberry. Hence, generality is difficult to achieve because a single pollinator trait, like big body size, may not lead to high pollination function in all contexts. Rather it seems likely that the most efficient trait will depend on the

crop (Garibaldi et al. 2015) and its degree of trait matching with the pollinator (Bartomeus et al. 2016). Moreover, the total pollination provided by a pollinator species is the product of visitation frequency and per capita efficiency (Kremen et al. 2007), two processes that may be governed by different traits. In fact, our finding here that the response–effect framework is not predictive is conservative in the sense that we measured the ‘effect’ directly attributable to native bee species, i.e. pollen deposition and visitation rates. If we had measured the downstream ecosystem service (fruit production) as the ‘effect,’ then pollination provided by managed honey bees likely would have obscured any association between response and effect traits even further.

Despite the conceptual elegance of the response–effect trait framework, it is only effective if it is predictive, and strong evidence for the generality of traits has not yet been found. A positive association between the response and effect traits (Naeem and Wright 2003) such that species with the strongest response to environmental change also have the strongest effect on function, indicates that land-use change has the potential for dramatic effects on ecosystem function. Whether response and effect traits are in general positively, negatively, or uncorrelated is an important question that has not yet been answered (Larsen et al. 2005). For example, even the very thorough and rigorously analyzed study of response–effect relationships by Larsen et al. (2005) is based on a non-significant weak relationship between pollinator per visit efficiency and body size. Similarly, the marginal  $R^2$  (i.e. variance explained by fixed effects) of the best model including traits in the comprehensive analysis done by De Palma et al. (2015) is lower than 0.1. Similarly, in our study, even the strongest correlations found for watermelon, where big species are less sensitive to local land-use change and more efficient per visit, but not more frequent flower visitors than smaller species, are too weak to be useful for predictive purposes.

Predictive response and/or effect traits are often assumed in the larger literature despite this lack of rigorous empirical evidence. For example, recent re-evaluations of community stability in food webs show that using body size as proxy of extinction risk changes the outcome of the stability simulations (Brose et al. 2017). However, the assumption that body size is a general predictor of extinction risk is not directly validated. Given the correlation showing that bigger species are more sensitive is usually weak (Fisher and Owens 2004). These kinds of approaches could produce misleading outcomes.

Alternatively, the response–effect framework itself might be robust, but the trait data themselves might be inadequate to reveal patterns. Currently trait data for wild bees may be too coarse to reveal ubiquitous response and effect traits for four reasons. First, some traits may simply reflect the identity of genera or higher taxonomic groups. For example, some bumble bee species in our three systems (especially *B. impatiens*) are common, functionally dominant, and robust to extinction (Cariveau et al. 2013, Winfree et al.

2015). Some of the response and effect traits that we could potentially have identified, such as cavity nesting, sociality and body size, may simply be proxies for bumble bees in our data sets. Therefore, studies that don't account for phylogenetic correlations may confound functional and phylogenetic responses (Li and Ives 2017). Second, traits may interact in complex ways and single traits may be not able to capture responses and functional contributions across species (Bommarco et al. 2010). Third, phenotypic variability within species, usually ignored in trait-based approaches, may play a more important role than previously thought (Bolnick et al. 2011). Finally, the most important traits may not have been studied. Response traits such as dispersal ability, fecundity, and nest microclimate/soil type, and effect traits like floral visitation behavior or hairiness (Stavert et al. 2016) may be better predictors than the traits we have now. However, if these traits are not easy to measure across bee species, they may be of little use. Traits databases that include an increasing number of traits and agreed-upon measurement techniques similar to those used in plant ecology (Kattge et al. 2011) but that are also open-access may lead to significant advancements in functional trait ecology in wild bees.

There is a call to be more predictive in ecology (Petchey et al. 2015, Houlahan et al. 2017). The use of traits to predict species responses and subsequent changes in ecosystem services is a potentially powerful approach. This is especially the case for organisms such as insects where species identification is challenging and detailed species-level natural history information is lacking. However, the ability to effectively use a trait framework is becoming controversial because studies thus far have not clearly related specific traits to specific threats or functions (Didham et al. 2016, Shipley et al. 2016). A growing number of studies are working to address the complexity and increase the predictability of this framework (Laughlin and Messier 2015). However, until these approaches yield consistent patterns across systems, site-specific species identity and monitoring may at present be the best measure for predicting changes in ecosystem services as a result of land-use change. A few dominant species often drive ecosystem functioning (Kleijn et al. 2015, Winfree et al. 2015). Identifying the sensitivity of the functionally dominant species may be the best proxy thus far for predicting effects of species loss in ecosystem function.

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Supplementary material (available online as Appendix oik-04507 at <[www.oikosjournal.org/appendix/oik-04507](http://www.oikosjournal.org/appendix/oik-04507)>). Appendix 1.