On the inconsistency of pollinator species traits for predicting either response to agricultural intensification or functional contribution.

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Running headline: Pollinator traits are not predictive

Abstract:

The response and effect trait framework, if supported empirically, would provide for powerful and general predictions about how biodiversity loss will lead 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 present detailed data on crop pollination services provided by native, wild bees to explore the role of six commonly used species traits in determining how crop pollination is affected by increasing agricultural intensification. 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 agricultural intensification, 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. So far, most studies looking for response or effect traits in pollination systems have found weak and often contradicting links. Overall we were unable to make generalizable predictions regarding species responses to land-use change and its effect on the delivery of ecosystem 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.

Keywords: Biodiversity, bees, ecosystem services, ecosystem function, response traits, effect traits, body size, diet specialism.

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

59 likely to be mediated by the species' traits ('effect traits'). Therefore, the
60 relationship between response and effect traits will mediate the magnitude of
61 the impact of human disturbance on ecosystem services (Schleuning et al.
62 2015). For example, if the same species traits that are associated with high
63 function are also most sensitive to disturbance, ecosystem function would be
64 predicted to decline rapidly (Larsen et al. 2005).

65 However, for the response-effect trait framework to be useful, it is first
66 necessary to identify response and effect traits that are both explanatory and
67 possible to measure in the field (Cadotte et al. 2011). While a few generalities
68 have emerged as to which traits make animal species at greater risk of local
69 decline, including dietary or habitat specialization and body size (Fisher and
70 Owens 2004, Flynn et al. 2009, Öckinger et al. 2010), the correlation between
71 these response traits and extinction risk has been found to be weak, variable,
72 or context-dependent (Devictor et al. 2008, Fritz et al. 2009, Powney et al.
73 2014). Similarly, although some effect traits have been identified, they are
74 often weakly predictive, and their identity varies by function and taxonomic
75 group (Gagic et al. 2015). Lastly, within the functional trait field as a whole,
76 most progress has been made in identifying functional traits for plants (Diaz et
77 al. 2016), while little is known for animals (Didham et al. 2016).

78 Here, we seek to identify response and effect traits for wild bee species
79 providing a key ecosystem service, crop pollination. The yield of most crop
80 plants increases with animal pollination (Klein et al. 2007). While managed
81 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). A major threat to pollinators is habitat destruction, primarily conversion to agriculture (Garibaldi et al. 2011), which is also a leading cause of species loss worldwide (Pereira et al. 2010). Thus agricultural land use has the potential to affect one of the ecosystem services upon which agriculture itself depends (Deguines et al. 2014).

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 agricultural intensification (response traits) and/or 2) species' contributions to crop pollination (effect traits) and discuss our results on 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 study systems that were located throughout New Jersey and eastern Pennsylvania (USA). Watermelon sites (N = 17) were located in 90 x 60 km region 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 x

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 and species richness. To collect bees, we walked along a fixed 50-200 m^2 transect at standard times of day and collected all bees observed to be visiting flowers. In watermelon and blueberry, bees were netted three times throughout the day for 20 minutes per transect (60 minutes per date per site) and twice each day in cranberry for 30 minutes per transect (120 minutes 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. Detailed methods can be found in Cariveau et

127 al. (2013), Benjamin et al. (2014) and Winfree et al. (2015).

128 *Land cover characteristics of sites*

129 To relate pollinator response traits to agricultural intensification we used a
130 commonly used land-use variable, percent land cover in agricultural
131 production surrounding sites (Fahrig 2013). For this end, we required high-
132 quality land cover data for each pollinator collection site. For the cranberry
133 and blueberry sites in New Jersey, we used a continuous polygon layer
134 classified by visual photograph interpretation into 60 categories, at a minimum
135 mapping unit of 4047 m^2 (1 acre; GIS Data provided by the New Jersey
136 Department of Environmental Protection). For watermelon sites that extend
137 from central New Jersey into Pennsylvania, we created a similar land cover
138 data layer by manually digitizing Google Earth imagery and visually classifying
139 15 categories, at a minimum mapping unit of 5,000 m^2 (1.24 acres). As each
140 crop was analyzed separately, our results are robust to using different land
141 cover data. However, to simplify the interpretation of results for the three
142 crops, we reclassified all land cover data into the following 7 broad categories:
143 agriculture, open managed (for example, mowed grass), open natural or semi-
144 natural (for example, old fields), semi-urban (<30% impervious surface), urban
145 (>30% impervious surface), wooded, and open water.

146 For each data collection site, we calculated two land cover variables: percent
147 agriculture and percent natural and semi-natural open habitat. We used
148 agricultural land cover as our primary land-use change variable as it is the
149 dominant anthropogenic habitat type in all three study systems

150 (Supplementary Table A1). In addition, we also measured percent of open
151 natural/semi-natural habitat, which although it accounts for only a small
152 proportion of the total land cover (Supplementary Table A1), might be
153 disproportionately important as forage and nesting habitat for bees (Kleijn et
154 al. 2006). We calculated values for this two land cover variables at both a
155 small scale (300 m radius) and a large scale (1500 m radius), which
156 correspond to typical flight distances of small- and large-bodied bees,
157 respectively (Greenleaf et al. 2007).

158 *Pollinator function*

159 To estimate the pollination services provided per bee species, we measured
160 two variables in the field, flower visitation frequency and per visit efficiency. As
161 variation in visitation frequency may be a function of land use at individual
162 farms, we use species abundances for each species at the site with its highest
163 abundance for each crop. Hence, we assess visitation frequency at its
164 maximum, which represents the optimal visitation frequency for each species.

165 To measure the pollination efficiency, we quantified single-visit pollen
166 deposition by presenting virgin flowers to individual bees foraging on the
167 target crop. After visitation, we counted the number of pollen grains deposited
168 per flower visit (watermelon) or the number of pollen tetrads with pollen tubes
169 per flower visit (cranberry and blueberry). Because species identification in the
170 field is not possible for most bees and net collecting immediately after visits is
171 generally not possible, for the measurement of pollination efficiency we
172 grouped bees in species groups. Each group consisted of between one and

173 27 species, with the median number of species per group being 4 species
174 (Supplementary Table A2). Control flowers were left bagged until the end of
175 the field day, and contained few pollen grains (watermelon mean = 3 grains, N
176 = 40 stigmas; cranberry mean = 0 tetrads, N = 82 stigmas; blueberry mean =
177 2 tetrads, N= 734 stigmas). We used mean number of pollen grains deposited
178 by a single visit group and assigned that value to each of the species in the
179 single visit group. For detailed methods see Cariveau et al. (2013), Benjamin
180 et al. (2014), Winfree et al. (2015).

181 *Species traits*

182 Bee species vary in a number of traits that are associated with their response
183 to land-use change (Williams et al. 2010). Moreover, these traits will likely
184 affect the pollinator contribution to function, either by modifying its abundance
185 or because they are related to its per capita effectiveness. We obtained
186 detailed natural history data on 6 traits for the 90 bee species in our study: a)
187 sociality (solitary, facultative social, eusocial), b) nesting placement (hole,
188 cavity, stem, wood, ground), c) brood parasite (yes, no), d) body size, e) diet
189 breadth (level of specialization) and f) tongue length.

190 We obtained the trait data as follows. Species sociality level, nesting behavior
191 and brood parasite status were extracted from the literature (Bartomeus et al.
192 2013a). Body size (estimated from intertegular span, IT; Cane 1987) was
193 measured in the lab using collected specimens that had been identified to the
194 species level by professional taxonomists. Multiple specimens were measured
195 per species (mean = 6.6 specimens ± 3 S.E.) and the mean across the

196 measured specimens was used as the value for the species. Bee body size
197 also correlates strongly with foraging distance (Greenleaf et al. 2007), and
198 thus is ecologically related to mobility. Tongue length was measured in the lab
199 for 7.7 ± 1.2 SE specimens per species, and the mean across the measured
200 specimens is used. For the 40 specimens for which we cannot obtain a
201 tongue measure, we estimated tongue length from the species' body size and
202 phylogeny using an allometric equation (Cariveau et al. 2016).

203 Diet breadth was calculated using six independent datasets previously
204 collected at 139 sites throughout the study region by the Winfree laboratory
205 group. Each data set consists of individual pollinator specimens that were net-
206 collected while foraging on a flowering plant species; both pollinator and plant
207 were then identified to the species level. Those datasets comprise overall 393
208 pollinator species, and 392 plant species, with 3890 plant-pollinator
209 interactions (Supplementary Text A1). Prior to calculating diet breadth, we
210 rarefied the data to 20 visitation records per bee species, to avoid
211 confounding rarity with specialization (Blüthgen et al. 2008; Winfree et al.
212 2014). Nine species had fewer than 20 records and we were unable to
213 estimate diet breadth in the manner described above. Five of these species
214 are known to be specialized and we simulated the diet breadth index of 20
215 individuals visiting the known host plants. The four other species are known to
216 be generalists and we therefore used the mean diet breadth of its genus.
217 These four species were extremely rare (< 5 records each) in our analyzed
218 dataset.

To calculate diet breadth for each bee species, we considered the number of plants species as well as the phylogenetic breadth that the bees fed upon by using a rarefied phylogenetic diversity index (Nipperess and Matsen 2013). To determine phylogenetic distances among plants, we first constructed a general phylogenetic tree using the PHYLOMATIC “megatree” (version R201120829, Chamberlain and Szöcs 2013) which defines relationships between 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).

Statistical analysis

Response traits: To investigate which traits are associated with environmental variables related to agricultural intensification, we used a model-based approach to the fourth-corner problem (Brown et al. 2014). The fourth-corner problem highlights the difficulty of studying the 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, being the relationships of this last corner 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

242 function of environmental variables, species traits and their interaction. The
243 environment-trait interaction coefficients can be understood as the fourth
244 corner and describes how environmental response across taxa varies as traits
245 vary. The size of coefficients is a measure of importance and are interpreted
246 as the amount by which a unit (1 sd) change in the trait variable changes the
247 slope of the relationship between abundance and a given environmental
248 variable. To estimate these coefficients, we used a LASSO-penalised
249 negative binomial regression (R package “mvabund”, Wang et al. 2012). The
250 LASSO penalty simplifies interpretation because it automatically does model
251 selection by setting to zero any interaction coefficients that do not help reduce
252 BIC. A species effect is included in the model (i.e. a different intercept term for
253 each species), so that traits are used to explain patterns in relative abundance
254 across taxa not patterns in absolute abundance. Pseudo-R2 is calculated as
255 the R2 of the predicted against the observed abundance values for each
256 species at each site.
257
258 **Effect trait analysis:** To determine which traits influenced functional
259 contribution of each species, we ran separate linear models with either
260 visitation or per capita efficiency as response variables. Species traits were
261 predictors. The best model based on AICc was selected. When differences
262 between the best models were less than 2 we selected the simpler model.
263 The analysis for efficiency was done at the species group level (see above:
264 pollination function section). To obtain traits at the species-group level, we
265 calculated the mean values over species belonging to the same group,

266 weighted by the species mean abundance within the group. For categorical
267 variables we chose the dominant level, again weighted by species
268 abundance. This way, we assure that while species within a functional group
269 are selected to be functionally similar, the average traits used reflects species
270 composition.

271 All residuals were visually inspected to validate model assumptions. All
272 statistical analyses were performed in R (version 3.0.3, <www.r-project.org>).

273 **Results**

274 **Response traits**: Overall, we did not find a strong correlation between any
275 ecological traits and the environmental variables analyzed despite finding a
276 general response of species abundance to change with one or more land use
277 variables (watermelon: estimate of percentage open habitat at 300m = 0.12;
278 blueberry: estimate of percentage agricultural habitat at 300 m= -0.26 and at
279 1500m = -0.12; cranberry: estimate percentage agricultural percentage habitat
280 at 1500m = -0.23. Supplementary Table A3). Traits do not modify these
281 slopes in most instances, and despite some traits exhibiting weak responses
282 to land use in some cases, these responses were not consistent across crops
283 (Fig 1). For watermelon (overall pseudo-R2 = 0.54), small bees and parasites
284 tended to decline with increasing percentage of agriculture at 300m radius
285 (Interaction estimate of % agriculture at 300m with body size = 0.19, Fig 1D;
286 and with Parasitism = 0.10) and parasites also declined with increasing open
287 areas at 1500m radius (interaction estimate = 0.13). For blueberry (overall
288 pseudo-R2 = 0.22) short-tongued species increased with increasing

289 agriculture at 1500m (interaction estimate = -0.30). In cranberry (overall
290 pseudo-R2 = 0.59), bees nesting in wood and generalist bees tended to
291 increase with increasing open areas at 300 m (interaction estimate = 0.14 and
292 0.11 respectively) and bees nesting in soil and bigger bees tend to increase
293 with increasing open areas at 1500 m buffer (interaction estimate = 0.14). A
294 complete list of all comparisons is presented in Supplementary material (Table
295 A3).

296 **Effect traits:** As for response traits, no traits were highly predictive of either
297 visitation frequency or per visit efficiency across crops. For watermelon, the
298 best model for visitation frequency does not includes any trait. However, per
299 visit efficiency was positively correlated with body size and tongue length (R2
300 = 0.75, F2,9 = 17.07, p < 0.001, Fig 2A). For cranberry, visitation frequency
301 was positively related to cavity nesters (R2 = 0.38, F4,36 = 7.1, p < 0.0001,
302 Fig 2B). This result was driven by *Bombus* species, which are the only cavity
303 nesters in this data set. In cranberry per visit efficiency was not related to any
304 trait. For blueberry, visitation frequency was positively related to diet
305 specialism (R2 = 0.37, F1,20 = 13.5, p = 0.001, Fig 2C), while efficiency per
306 visit is positively related to tongue length (R2 = 0.70, F1,5 = 14.9, p = 0.01,
307 Fig 2D). Model selection, can be found in Supplementary material (Table A4).

308 **Discussion:**

309 Identifying traits that characterize which species are more sensitive to land-
310 use change or those that are functionally important is complex. We found
311 some evidence for response and effect traits but they differed among crop

312 species as well as landscape variable used. Therefore, while some traits may
313 be important in some contexts, no traits were generalizable enough to be
314 used to predict how land-use change will influence the delivery of pollination
315 services across these systems. Further, the relationships identified were
316 weak. This does not negate the importance of traits for understanding which
317 mechanisms underlie species responses to land-use change or pollination
318 effectiveness, but it does suggest that traits commonly used for wild bees
319 might not be suitable for predicting which species will decline or how land-use
320 change will influence the delivery of ecosystem services. In fact, the trait-
321 based literature in general is characterized by weak and/or idiosyncratic
322 relationships between traits and either species responses and functional
323 effects (Tables 1 and 2).

324 Being able to identify strong response traits would be a key tool for
325 understanding extinction risk, and an asset for conservation planning.
326 However, characterizing extinction risk based on traits is challenging. Despite
327 some generalities that emerge across taxa, with rare species, big species,
328 specialists, and higher trophic levels being in general more sensitive to
329 disturbances (Fisher and Owens 2004), there is a large variation in the
330 response of the species with those traits (Fritz et al. 2009; Seguin et al. 2014).
331 Work specifically on native bees has found that traits such as specialization,
332 body size, and sociality may predict responses to land use (Table 1; Winfree
333 et al. 2009, Bommarco et al. 2010, Williams et al. 2010, Bartomeus *et al.*
334 2013b, Kremen and M'Gonigle 2015, De Palma et al. 2015, Carrié et al.
335 2016). However, studies often find contrasting results (Table 1). For example,

336 De Palma et al. (2015) analyzed over 70,000 wild bee records and found that
337 small species were most sensitive to agricultural land use, while others have
338 found that larger species are more sensitive to agricultural land use and/or
339 environmental change generally (Larsen et al. 2005; Bartomeus et al. 2013b),
340 and some have found little effect of body size (Williams et al. 2010). Here, we
341 found a weak trend for small species to be more sensitive to local agricultural
342 intensification in watermelon, but this trend disappears when land use is
343 measured at larger scales. Another trait, dietary specialization, is one of the
344 few traits that has been generally linked to increased species sensitivity to
345 environmental change (Table 1, Williams et al. 2010; Scheper et al. 2014; De
346 Palma et al. 2015), but here we found that floral specialist bees did not decline
347 with intensifying agriculture. If anything, one of the most abundant bee
348 species in the cranberry system (*Mellita americana*) is a specialist on
349 cranberry (*Vaccinium macrocarpon*). Specialist bees observed in crop
350 systems are likely to be specialized on the crop plant family as was the case
351 in our data (e.g. *Mellita americana* in cranberry, but also *Habropoda sp.* and
352 *Andrena bradleyi* in blueberry and *Peponapis pruinosa* in watermelon). We
353 would expect different responses from study designs that include natural
354 habitat and a larger range of specialist host plants (Forrest et al. 2015,
355 Bartomeus and Winfree 2013).
356
357 Alternatively, the lack of strong trait-environment associations may be due to
358 the variables used to measure agricultural intensification being too coarse to
359 detect common responses. While finer-resolution studies will undoubtedly be

360 informative, they are unlikely to lead to a greater likelihood of predicting how
361 changes in biodiversity affects the delivery of ecosystem services if these
362 measures are difficult to quantify or are context dependent.

363 Effect traits have been even harder to identify for pollinators. The limited data
364 published on particular plants suggests insects with larger bodies tend to
365 deposit more pollen per flower visit, but this pollen was not well distributed on
366 the stigma (Table 2; Hoehn et al. 2008), or that the correlation between body
367 size and per visit pollination function is low (Larsen et al. 2005). Our study
368 supports the positive correlation between body size and per-visit pollen
369 deposition in both watermelon and blueberry (although note that tongue
370 length is correlated with body size in blueberry r = 0.76), but not for cranberry.
371 Hence, generality is difficult to achieve because a single pollinator trait, like
372 big body size, may not lead to high pollination function in all contexts. Rather it
373 seems likely that the most efficient trait will depend on the crop (Garibaldi et
374 al. 2015). Moreover, the total pollination provided by a pollinator species is the
375 product of visitation frequency and per capita efficiency (Kremen et al. 2005),
376 two processes that may be governed by different traits.

377 If generalizable response and effect traits can be found, the final step will be
378 to link response and effects to predict changes in ecosystem services. A
379 positive association between the response and effect traits (Naeem and
380 Wright 2003) such that species with the strongest response to environmental
381 change also had the strongest effect on function, indicates the land-use
382 change has the potential for dramatic effects on ecosystem function. Whether

383 response and effect traits are in general positively, negatively, or uncorrelated
384 is an important question that has not yet been answered (Larsen et al. 2005).
385 Despite the conceptual elegance of the response-effect trait framework, it is
386 only effective if it is predictive, and strong evidence for the generality of traits
387 has not yet been found. For example, even the very thorough and rigorously
388 analyzed study of response-effect relationships by Larsen et al. (2005) is
389 based on a non-significant weak relationship between pollinator per visit
390 efficiency and body size. Similarly, the marginal R^2 (i.e. variance explained by
391 fixed effects) of the best model including traits in the comprehensive analysis
392 done by De Palma et al. (2015) is lower than 0.1. Similarly, in our study, even
393 the strongest correlations found for watermelon, where big species are less
394 sensitive to local agricultural intensification and more efficient per visit, but not
395 more frequent flower visitors than smaller species are too weak to be useful
396 for predictive purposes.

397 Predictive response and/or effect traits are often assumed in the larger
398 literature as well. For example, recent re-evaluations of community stability in
399 food webs shows that using body size as proxy of extinction risk changes the
400 outcome of the stability simulations (Brose et al. 2016). However, the
401 assumption that body size is a good predictor of extinction risk is not directly
402 validated. Given the correlation showing that bigger species are more
403 sensitive is usually weak (Fisher and Owens 2004), these kind of approaches
404 could produce misleading outcomes.

405 Currently trait data may be too coarse to reveal ubiquitous response and

406 effect traits for four reasons. First, some traits may simply reflect identity of
407 genera or higher taxonomic groups. For example, some bumble bee species
408 in our three systems (especially *B. impatiens*) are common, functionally
409 dominant, and robust to extinction (Cariveau et al. 2013, Winfree et al. 2015).
410 Some of the important response and effect traits that we found, such as cavity
411 nesting and body size, may simply be proxies for bumble bees. Bumble bee
412 species also share other traits (e.g. sociality) that are commonly used in trait
413 analyses. Therefore, studies that don't include phylogenetic correlations may
414 be simply characterizing the general relationship between disturbance and the
415 functionally dominant taxa. As there is a great variability in the responses to
416 disturbance among bumble bee species (Cameron et al. 2011; Bartomeus et
417 al. 2013b, Persson et al. 2015) this may also explain why some studies find
418 big species to be more sensitive to land-use change (Larsen et al. 2005) and
419 other studies find the opposite (Rader et al. 2014, this study for watermelon).
420 Second, traits may interact in complex ways and single traits may be not able
421 to capture responses and functional contributions across species (e.g.
422 Bommarco et al. 2010). Third, phenotypic variability within species, usually
423 ignored in trait-based approaches, may play a more important role than
424 previously though (Bolnik et al. 2011). Finally, the most important traits may
425 not have been studied. Response traits such as dispersal ability, fecundity,
426 and nest microclimate/soil type, and effect traits like floral visitation behavior
427 or hairiness (Stavert et al. 2016) may be better predictors than the traits we
428 have now. However, if these traits are not easy to measure across bee
429 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. 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 (e.g. 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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Data Accessibility: All data and code used in this manuscript is accessible in github (https://github.com/ibartomeus/RE_traits) and will be archived on acceptance in figshare.

References:

Bartomeus, I. and Winfree, R. 2013. Pollinator declines: reconciling scales and implications for ecosystem services. - F1000Res. 2: 146.
Bartomeus, I. et al. 2013a. Data from: Historical changes in northeastern US bee pollinators related to shared ecological traits.
Bartomeus, I. et al. 2013b. Historical changes in northeastern US bee pollinators related to shared ecological traits. - Proc. Natl. Acad. Sci. U. S. A. 110: 4656–4660.
Beaulieu, J. M. et al. 2007. Genome size evolution in relation to leaf strategy and metabolic rates revisited. - Ann. Bot. 99: 495–505.
Benjamin, F. E. et al. 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. - J. Appl. Ecol. 51: 440–449.
Blüthgen, N. et al. 2008. What do interaction network metrics tell us about specialization and biological traits? - Ecology 89: 3387–3399.
Bolnick, D. I. et al. 2011. Why intraspecific trait variation matters in community ecology. - Trends Ecol. Evol. 26: 183–192.
Bommarco, R. et al. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. - Proc. Biol. Sci. 277: 2075–2082.
Brose, U. et al. 2016. Predicting the consequences of species loss using size-structured biodiversity approaches. - Biol. Rev. Camb. Philos. Soc. in press.
Brown, A. M. et al. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. - Methods Ecol. Evol. 5: 344–352.
Cadotte, M. W. et al. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. - J. Appl. Ecol. 48: 1079–1087.
Cameron, S. A. et al. 2011. Patterns of widespread decline in North American bumble bees. - Proc. Natl. Acad. Sci. U. S. A. 108: 662–667.
Cane, J. 1987. Estimation of bee size using intertegular span (Apoidea). - J. Kans. Entomol. Soc. 60: 145–147.
Cane, J. et al. 2006. Multiple response of desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. - Ecol. Appl. 16: 632–644.
Cardinale, B. J. et al. 2012. Biodiversity loss and its impact on humanity. - Nature 486: 59–67.

Cariveau, D. P. et al. 2013. Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators. - Ecol. Lett. 16: 903–911.
Cariveau, D. P. et al. 2016. The allometry of bee proboscis length and its uses in ecology. - PLoS One 11: e0151482.
Carrié, R. et al. 2017. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. - Ecography 40: 85–97.
Chamberlain, S. A. and Szöcs, E. 2013. taxize: taxonomic search and retrieval in R. - F1000Res. 2: 191.
Deguines, N. et al. 2014. Large-scale trade-off between agricultural intensification and crop pollination services. - Front. Ecol. Environ. 12: 212–217.
De Palma, A. et al. 2015. Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. - J. Appl. Ecol. 52: 1567–1577.
Devictor, V. et al. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. - Oikos 117: 507–514.
Díaz, S. et al. 2016. The global spectrum of plant form and function. - Nature 529: 167–171.
Didham, R. K. et al. 2016. Circle the bandwagons – Challenges mount against the theoretical foundations of applied functional trait and ecosystem service research. - Insect Conserv. Divers. 9: 1–3.
Ellis, E. C. et al. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. - Glob. Ecol. Biogeogr. 19: 589–606.
Fisher, D. O. and Owens, I. P. F. 2004. The comparative method in conservation biology. - Trends Ecol. Evol. 19: 391–398.
Flynn, D. F. B. et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. - Ecol. Lett. 12: 22–33.
Forrest, J. R. K. et al. 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. - J. Appl. Ecol. 52: 706–715.
Fritz, S. A. et al. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. - Ecol. Lett. 12: 538–549.
Gagic, V. et al. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. - Proceedings of the Royal Society of London B: Biological Sciences 282: 20142620.
Garibaldi, L. A. et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. - Ecol. Lett. 14: 1062–1072.
Garibaldi, L. A. et al. 2015. Trait matching of flower visitors and crops predicts fruit set better than trait diversity. - J. Appl. Ecol. 52: 1436–1444.
Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. - Oecologia 153: 589–596.
Hoehn, P. et al. 2008. Functional group diversity of bee pollinators increases crop yield. - Proc. Biol. Sci. 275: 2283–2291.

539 Houlahan et al. 2017. The priority of prediction in ecological understanding. -
540 Oikos 126: 1-7.
541 Jauker B. et al. 2013. Linking life history traits to pollinator loss in fragmented
542 calcareous grasslands. - Landscape Ecol. 28:107-120.
543 Kattge, J. et al. 2011. TRY--a global database of plant traits. - Glob. Chang.
544 Biol. 17: 2905–2935.
545 Kleijn, D. et al. 2006. Mixed biodiversity benefits of agri-environment schemes
546 in five European countries: Biodiversity effects of European agri-
547 environment schemes. - Ecol. Lett. 9: 243–254.
548 Kleijn, D. et al. 2015. Delivery of crop pollination services is an insufficient
549 argument for wild pollinator conservation. - Nat. Commun. 6: 7414.
550 Klein, A.-M. et al. 2007. Importance of pollinators in changing landscapes for
551 world crops. - Proc. Biol. Sci. 274: 303–313.
552 Klein, A.-M. et al. 2008. Advances in pollination ecology from tropical
553 plantation crops. - Ecology 89: 935–943.
554 Kremen, C. 2005. Managing ecosystem services: what do we need to know
555 about their ecology? - Ecol. Lett. 8: 468–479.
556 Kremen, C. and M'Gonigle, L. K. 2015. Small-scale restoration in intensive
557 agricultural landscapes supports more specialized and less mobile
558 pollinator species. - J. Appl. Ecol. 52: 602–610.
559 Larsen, T. H. et al. 2005. Extinction order and altered community structure
560 rapidly disrupt ecosystem functioning. - Ecol. Lett. 8: 538–547.
561 Laughlin, D. C. and Messier, J. 2015. Fitness of multidimensional phenotypes
562 in dynamic adaptive landscapes. - Trends Ecol. Evol. 30: 487–496.
563 Lavorel, S. and Garnier, E. 2002. Predicting changes in community
564 composition and ecosystem functioning from plant traits: revisiting the
565 Holy Grail. - Funct. Ecol. 16: 545–556.
566 Legendre, P. et al. 1997. Relating behavior to habitat: Solutions to the fourth-
567 corner problem. - Ecology 78: 547–562.
568 McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. -
569 Trends Ecol. Evol. 21: 178–185.
570 Naeem, S. and Wright, J. P. 2003. Disentangling biodiversity effects on
571 ecosystem functioning: deriving solutions to a seemingly insurmountable
572 problem. - Ecol. Lett. 6: 567–579.
573 Nipperess, D. A. and Matsen 4, F. A. 2013. The mean and variance of
574 phylogenetic diversity under rarefaction. - Methods Ecol. Evol. 4: 566–
575 572.
576 Öckinger, E. et al. 2010. Life-history traits predict species responses to habitat
577 area and isolation: a cross-continental synthesis. - Ecol. Lett. 13: 969–
578 979.
579 Pereira, H. M. et al. 2010. Scenarios for global biodiversity in the 21st century.
580 - Science 330: 1496–1501.
581 Persson, A. S. et al. 2015. Bumble bees show trait-dependent vulnerability to
582 landscape simplification. - Biodivers. Conserv. 24: 3469–3489.
583 Petchey, O. L. et al. 2015. The ecological forecast horizon, and examples of
584 its uses and determinants. - Ecol. Lett. 18: 597–611.

Powney, G. D. et al. 2014. Can trait-based analyses of changes in species distribution be transferred to new geographic areas? - Glob. Ecol. Biogeogr. 23: 1009–1018.
Rader, R. et al. 2014. The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. - Divers. Distrib. 20: 908–917.
Rader, R. et al. 2016. Non-bee insects are important contributors to global crop pollination. - Proc. Natl. Acad. Sci. U. S. A. 113: 146–151.
Scheper, J. et al. 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. - Proc. Natl. Acad. Sci. U. S. A. 111: 17552–17557.
Schleuning, M. et al. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant--animal interactions. - Ecography 38: 380–392.
Schwartz, M. W. et al. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. - Oecologia 122: 297–305.
Séguin, A. et al. 2014. Body size as a predictor of species loss effect on ecosystem functioning. - Sci. Rep. 4: 4616.
Shipley, B. et al. 2016. Reinforcing loose foundation stones in trait-based plant ecology. - Oecologia 180: 923–931.
Stavert, J. R. et al. 2016. Hairiness: the missing link between pollinators and pollination. - PeerJ 4: e2779.
Wang, Y. et al. 2012. mvabund - an R package for model-based analysis of multivariate abundance data: The mvabund R package. - Methods Ecol. Evol. 3: 471–474.
Webb 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. - Am. Nat. 156: 145.
Webb, C. O. et al. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. - Bioinformatics 24: 2098–2100.
Wikstrom, N. et al. 2001. Evolution of the angiosperms: calibrating the family tree. - Proceedings of the Royal Society B: Biological Sciences 268: 2211–2220.
Williams, N. M. et al. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. - Biol. Conserv. 143: 2280–2291.
Winfree, R. et al. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. - Ecology 90: 2068–2076.
Winfree, R. et al. 2014. Species abundance, not diet breadth, drives the persistence of the most linked pollinators as plant-pollinator networks disassemble. - Am. Nat. 183: 600–611.
Winfree, R. et al. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. - Ecol. Lett. 18: 626–635.

Tables and Figures

Table 1: Summary of some recent studies identifying response traits and its relationship with environmental variables. Environmental variables have been grouped in two main categories because each study uses different metrics. Habitat loss (e.g. isolation, % natural habitat, habitat fragment size) and Agricultural intensification (e.g. natural vs agricultural, % agriculture). Only the direction of the response is indicated, as the different analysis makes any comparison of effect sizes meaningless. Note that in addition, most of this relationships are weakly predictive. See text for details.

		Relationship direction			
Trait	**Environment**	**Positive**	**Neutral**	**Negative**	**Context dependent**
Body size	Habitat loss	0	1[9]	2[1,10]	1[2]
	Agricultural intensification	2[7,11]	2[3,6]	4[1,4,5,8]	0
Diet specialization	Habitat loss	1[3]	0	2[1,9]	1[2]
	Agricultural intensification	0	1[8,6]	4[3,7]	0
Sociality (social)	Habitat loss	0	1[2]	1[3]	1[10]
	Agricultural intensification	4[3,4,8]	2[6,7]	0	0
Nest location (below-ground)	Habitat loss	0	1[3]	0	0
	Agricultural intensification	0	2[3,6]	2[8,11]	1[7]

[1]Larsen *et al.* 2005, [2]Bommarco et al. 2010, [3]Williams et al. 2010, [4]Rader et al. 2014, [5]Benjamin et al. 2014, [6]Forrest et al. 2015, [7]De Palma et al. 2015, [8]Carrié et al. 2016, [9]Cane

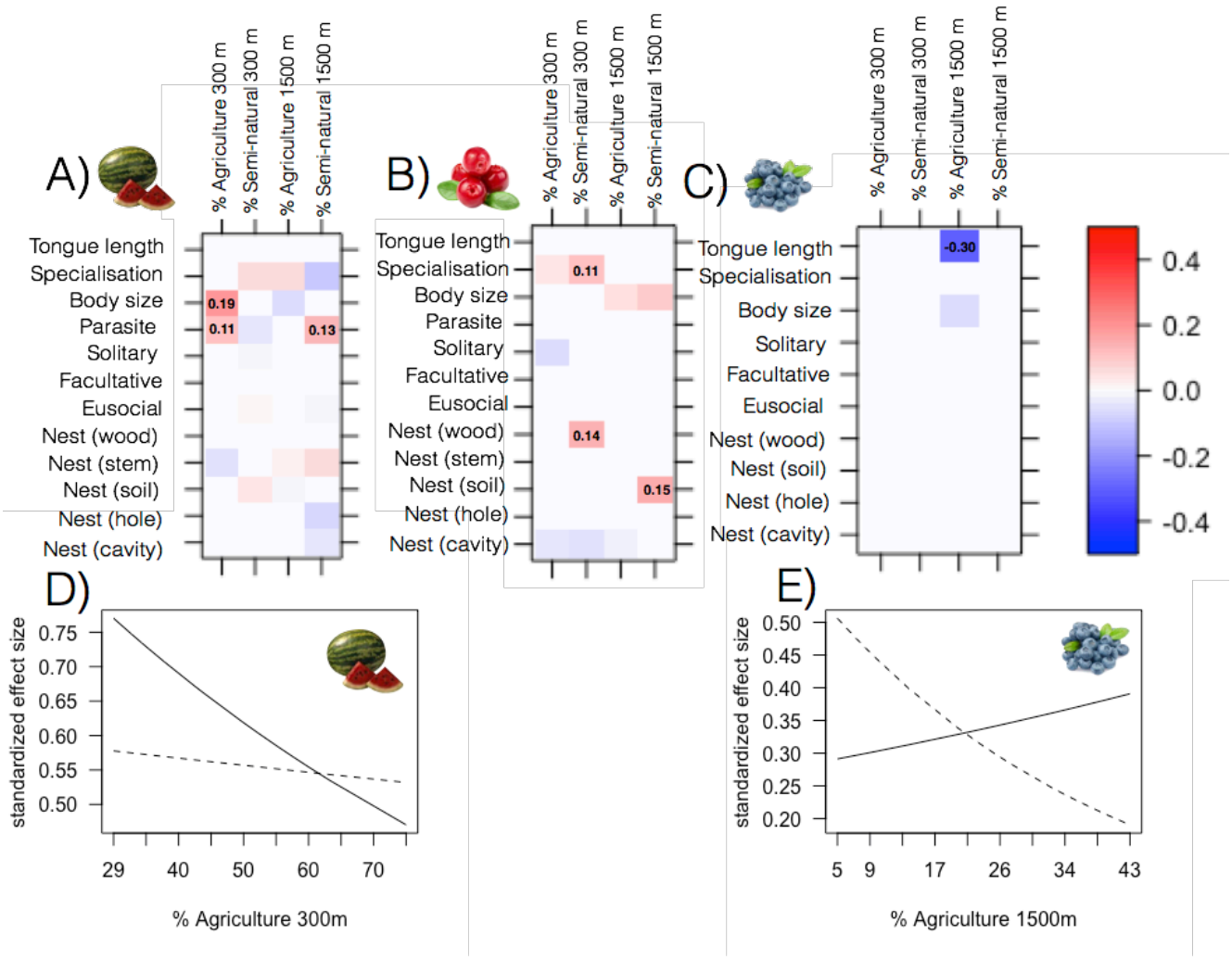
641 et al. 2006, [10]Jauker et al. 2013, [11]Klein et al 2008.

642 **Table 2:** Summary of some recent studies identifying effect traits and its
643 relationship with ecosystem functioning. Only body size is included, as other
644 traits are rarely measured (but see Stavert et al 2016 for hairiness). Only the
645 direction of the response is indicated, as the different analysis makes any
646 comparison of effect sizes meaningless. Note that in addition, most of these
647 relationships are weakly predictive. See text for details.

		Relationship direction			
Trait	**Function**	**Positive**	**Neutral**	**Negative**	**Context dependent**
Body size	Pollen deposition	2[1,2]	1[3]	0	0
	Visitation rate	0	0	1[2]	0
	Fruit set	0	0	0	2[4,5]

648 [1]Larsen *et al.* 2010, [2]Hohen et al. 2008, [3]Stavert et al. 2016, [4]Garibaldi et al. 2015, [5]Gagic et
649 al. 2015

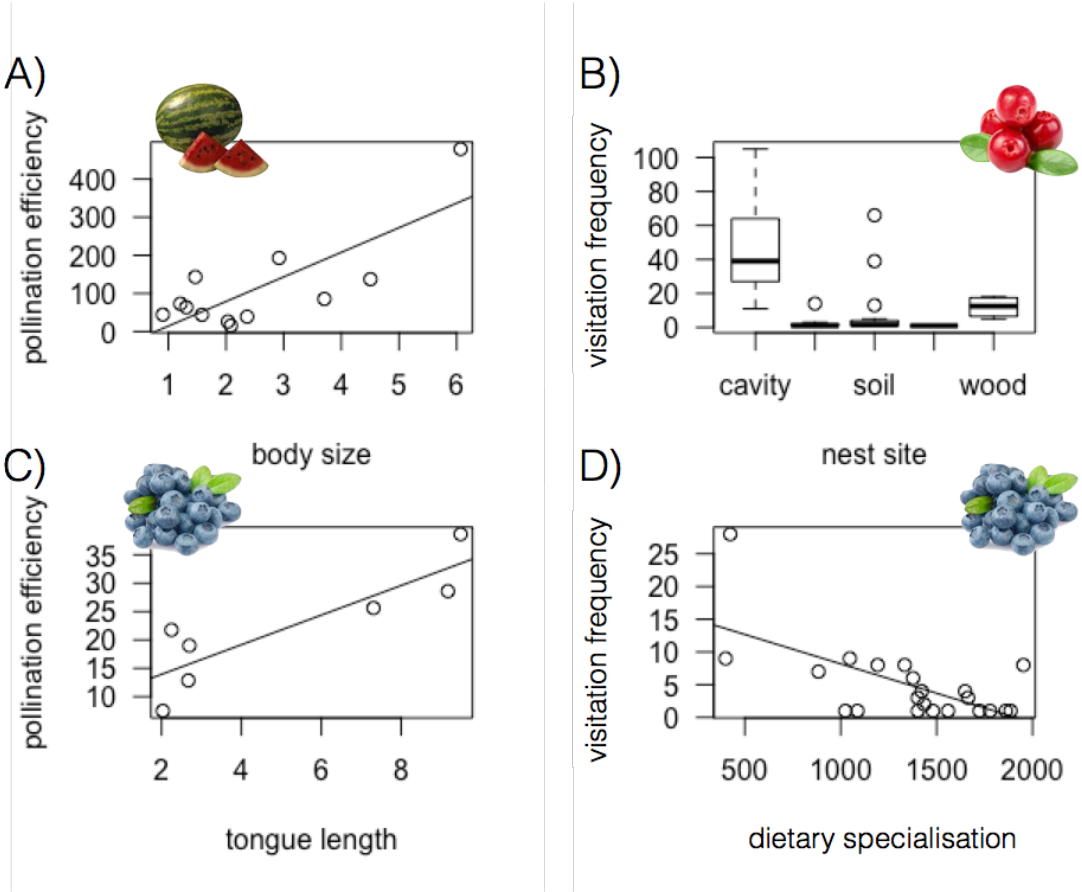
650 **Fig. 1: Relationships between traits and environmental variables** for A)
651 watermelon, B) blueberry and c) cranberry. Positive estimates are in red and
652 negative estimates in blue. Note that the LASSO penalty has set many
653 estimates to zero. D) Detail of the two stronger interactions between body size
654 and percentage of agriculture at 300 meter radii for watermelon and tongue
655 length and % of agriculture at 1500 meter for blueberry. The solid line is the
656 prediction for the 25 percentile of body size and tongue length, while the
657 dashed line is the prediction for the 75% of body size and tongue length for
658 watermelon and blueberry respectively.


A)
B)
C)
% Agriculture 300 m
% Semi-natural 300 m
% Agriculture 1500 m
% Semi-natural 1500 m
Tongue length
Specialisation
Body size
Parasite
Solitary
Facultative
Eusocial
Nest (wood)
Nest (stem)
Nest (soil)
Nest (hole)
Nest (cavity)
0.19
0.11
0.13
0.11
0.14
0.15
-0.30
0.4
0.2
0.0
-0.2
-0.4
D)
E)
standardized effect size
% Agriculture 300m
% Agriculture 1500m

659

660

Fig. 2: Multipanel plot showing the relationships between species traits and pollination function, which is decomposed into efficiency (pollen deposited per flower visit) and frequency of flower visits. A) watermelon, B) cranberry, C-D) blueberry.



667 **Supplementary material**

668 **Text A1:** Datasets used for calculating dietary specialization: Six datasets
669 were used to create the phylogenetic distance index. All data were collected in
670 the region of the crop study. Specimens were collected using a hand net and
671 the bee species and plant species were recorded. This resulted in a total of
672 18,733 bee x plant interactions for species that were also in the crop dataset.
673 The number of species, sites, and years of collection are as follows: 1) Pine
674 barrens in 2003: 280 bee x plant interactions. Habitat types were extensive
675 pine-oak forest (14 sites), forest fragments (14 sites), suburban back yards (7
676 sites), and agricultural field borders (5 sites) in New Jersey (Winfree et al.
677 2007). Bees were collected in temporally stratified sampling rounds between
678 April and September. 2) NJPA: 3906 bee x plant interactions. Data collected
679 on watermelon field margins at a total of 20 sites. Farm types included small-
680 scale mixed farming, both crops and field margins, both organic and low-
681 pesticide-input conventional. All bees were collected in three temporally
682 stratified sampling rounds in July, in each of 3 years. 3) NFWF 3906 bee x
683 plant interactions. Habitat types were old fields. Bees were collected in May
684 through Sept at 25 sites for two years. *Lasioglossum* species where not
685 included for this dataset due to recent changes in its taxonomy. 4) NSF 2006
686 666 bee x plant interactions. Habitat types were deciduous forest fragments
687 (13 sites), and suburban / urban yards (3 sites) and sites with extensive
688 forests with diverse wildflower communities (4 sites). All bees were collected
689 in sampling rounds between April and early June. 5) CIG 4600 bee x plant
690 interactions. Site were comprised of old fields as well as pollinator

enhancement sites. Bees using were collected using a hand net from a total of a total 18 sites in 2011-2013. For each bee specimen, the plant species was recorded. 6) Cape May 5858 bee x plant interactions. This study included only one site. The habitat was an old field that had been planted in 20 species of native perennial plants. Sampling took place over 3 years in sampling rounds that occurred in May through September.

Winfree, R. Griswold, T. and Kremen, C. (2007). Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*. 21: 213-223.

Table A1: Range of variation in agricultural and semi-natural land cover for three crop systems

	Percent Agriculture				Percent Natural, Open			
	Radius 300 m		Radius 1500 m		Radius 300 m		Radius 1500 m	
Crop	Min	Max	Min	Max	Min	Max	Min	Max
Watermelon	29	75	5	42	0	20	1	15
Blueberry	37	100	13	81	0	16	0.5	9
Cranberry	37	99	5	48	0	38	4	13

Table A2: Equivalencies between species and groups used for single visit data.

Crop	Species	Single Visit Group	Percentage

			within group
Blueberry	*Andrena_banksi*	MED_AND	0.00
Blueberry	*Andrena_barbara*	MED_AND	0.00
Blueberry	*Andrena_bradleyi*	MED_AND	0.93
Blueberry	*Andrena_carlini*	LG_AND	0.12
Blueberry	*Andrena_carolina*	LG_AND	0.01
Blueberry	*Andrena_cressonii*	LG_AND	0.01
Blueberry	*Andrena_fenningeri*	MED_AND	0.01
Blueberry	*Andrena_hilaris*	MED_AND	0.00
Blueberry	*Andrena_ilicis*	MED_AND	0.00
Blueberry	*Andrena_imitatrix*	MED_AND	0.01
Blueberry	*Andrena_mandibularis*	MED_AND	0.00
Blueberry	*Andrena_morrisonella*	MED_AND	0.01
Blueberry	*Andrena_screpteropsis*	MED_AND	0.00
Blueberry	*Andrena_vicina*	LG_AND	0.86
Blueberry	*Augochlora_pura*	Green	0.56
Blueberry	*Augochlorella_aurata*	Green	0.44
Blueberry	*Bombus_bimaculatus*	Bom_Q	0.24
Blueberry	*Bombus_griseocollis*	Bom_Q	0.49
Blueberry	*Bombus_impatiens*	Bom_Q	0.18
Blueberry	*Bombus_perplexus*	Bom_Q	0.08
Blueberry	*Ceratina_calcarata/dupla*	Dialictus	0.22
Blueberry	*Colletes_inaequalis*	Coll	0.26
Blueberry	*Colletes_thoracicus*	Coll	0.09
Blueberry	*Colletes_validus*	Coll	0.65
Blueberry	*Habropoda_laboriosa*	HAB	1.00
Blueberry	*Lasioglossum_acuminatum*	Small-dark	0.02
Blueberry	*Lasioglossum_coeruleum*	Small-dark	0.02
Blueberry	*Lasioglossum_fuscipenne*	Small-dark	0.02
Blueberry	*Lasioglossum_leucocomum*	Small-dark	0.02
Blueberry	*Lasioglossum_oblongum*	Small-dark	0.10
Blueberry	*Lasioglossum_pilosum*	Small-dark	0.15
Blueberry	*Lasioglossum_versatum*	Small-dark	0.02
Blueberry	*Lasioglossum_weemsi*	Small-dark	0.07
Blueberry	*Lasioglossum_zephyrum*	Small-dark	0.05
Blueberry	*Nomada_luteola*	Small-dark	0.02
Blueberry	*Osmia_taurus*	Small-dark	0.02
Blueberry	*Osmia_cornifrons*	Small-dark	0.02
Blueberry	*Osmia_pumila*	Small-dark	0.07
Blueberry	*Sphecodes_aroniae*	Small-dark	0.02
Blueberry	*Sphecodes_stygius*	Small-dark	0.02
Blueberry	*Xylocopa_virginica*	XYL	1.00
Cranberry	*Agapostemon_splendens*	Green	0.02
Cranberry	*Andrena_cressonii*	Med_and	0.01

Cranberry	*Andrena_imitatrix*	Med_and	0.01
Cranberry	*Andrena_morrisonella*	Med_and	0.01
Cranberry	*Andrena_spiraeana*	Med_and	0.01
Cranberry	*Andrena_vicina*	Med_and	0.02
Cranberry	*Augochlora_pura*	Green	0.16
Cranberry	*Augochlorella_aurata*	Green	0.63
Cranberry	*Augochloropsis_metallica*	Green	0.16
Cranberry	*Augochloropsis_sumptuosa*	Green	0.03
Cranberry	*Bombus_bimaculatus*	Bombus_bimaculatus	1.00
Cranberry	*Bombus_citrinus*	Bombus_spp	0.50
Cranberry	*Bombus_griseocollis*	Bombus_griseocollis	1.00
Cranberry	*Bombus_impatiens*	Bombus_impatiens	1.00
Cranberry	*Bombus_perplexus*	Bom_pervag	0.85
Cranberry	*Bombus_sandersoni*	Bombus_spp	0.50
Cranberry	*Bombus_vagans*	Bom_pervag	0.15
Cranberry	*Ceratina_calcarata/dupla*	Small_black	0.12
Cranberry	*Coelioxys_immaculata*	Megachile	0.02
Cranberry	*Coelioxys_porterae*	Megachile	0.04
Cranberry	*Coelioxys_sayi*	Megachile	0.02
Cranberry	*Colletes_consors*	Megachile	0.02
Cranberry	*Halictus_rubicundus*	Small_black	0.02
Cranberry	*Heriades_carinatus*	Osmia	0.08
Cranberry	*Hoplitis_truncata*	Osmia	0.12
Cranberry	*Hylaeus_affinis*	Small_black	0.08
Cranberry	*Lasioglossum_apopkense*	Small_black	0.01
Cranberry	*Lasioglossum_coeruleum*	Small_black	0.01
Cranberry	*Lasioglossum_creberrimum*	Small_black	0.02
Cranberry	*Lasioglossum_fuscipenne*	Small_black	0.05
Cranberry	*Lasioglossum_georgeickworti*	Small_black	0.05
Cranberry	*Lasioglossum_lineatulum*	Small_black	0.01
Cranberry	*Lasioglossum_oblongum*	Small_black	0.15
Cranberry	*Lasioglossum_pilosum*	Small_black	0.02
Cranberry	*Lasioglossum_planatum*	Small_black	0.02
Cranberry	*Lasioglossum_subviridatum*	Small_black	0.17
Cranberry	*Lasioglossum_trigeminum*	Small_black	0.02
Cranberry	*Lasioglossum_versatum*	Small_black	0.04
Cranberry	*Megachile_addenda*	Megachile	0.22
Cranberry	*Megachile_gemula*	Megachile	0.32
Cranberry	*Megachile_mendica*	Megachile	0.28
Cranberry	*Megachile_texana*	Megachile	0.08
Cranberry	*Melitta_americana*	Melitta	0.95
Cranberry	*Nomada_bella/lepida*	Small_black	0.01
Cranberry	*Nomada_pygmaea*	Small_black	0.01
Cranberry	*Nomada_rodecki*	Small_black	0.07

Cranberry	*Osmia_inspergens*	Osmia	0.07
Cranberry	*Osmia_pumila*	Osmia	0.13
Cranberry	*Osmia_virga*	Osmia	0.60
Cranberry	*Panurginus_atramontensis*	Small_black	0.09
Cranberry	*Sphecodes_aroniae*	Small_black	0.03
Cranberry	*Sphecodes_fattigi*	Small_black	0.01
Cranberry	*Xylocopa_virginica*	XYL	1.00
Watermelon	*Agapostemon_sericeus*	Large_Green	0.25
Watermelon	*Agapostemon_texanus*	Large_Green	0.11
Watermelon	*Agapostemon_virescens*	Large_Green	0.52
Watermelon	*Anthidium_oblongatum*	LDS	0.03
Watermelon	*Augochlora_pura*	Small_Green	0.80
Watermelon	*Augochlorella_aurata*	Small_Green	0.20
Watermelon	*Augochloropsis_metallica*	Large_Green	0.11
Watermelon	*Bombus_bimaculatus*	BOM	0.01
Watermelon	*Bombus_fervidus*	BOM	0.00
Watermelon	*Bombus_griseocollis*	BOM	0.01
Watermelon	*Bombus_impatiens*	BOM	0.98
Watermelon	*Bombus_perplexus*	BOM	0.00
Watermelon	*Bombus_vagans*	BOM	0.00
Watermelon	*Calliopsis_andreniformis*	SD	0.03
Watermelon	*Ceratina_calcarata/dupla*	CER	0.81
Watermelon	*Ceratina_strenua*	CER	0.19
Watermelon	*Halictus_confusus*	HAL_MDS	0.83
Watermelon	*Halictus_ligatus*	HAL_MDS	0.16
Watermelon	*Halictus_parallelus*	LDS	0.03
Watermelon	*Halictus_rubicundus*	LDS	0.56
Watermelon	*Hoplitis_pilosifrons*	HAL_MDS	0.00
Watermelon	*Hoplitis_producta*	HAL_MDS	0.00
Watermelon	*Hylaeus_affinis*	TD	0.01
Watermelon	*Lasioglossum_admirandum*	SD	0.01
Watermelon	*Lasioglossum_albipenne*	SD	0.00
Watermelon	*Lasioglossum_atwoodi*	SD	0.00
Watermelon	*Lasioglossum_bruneri*	SD	0.01
Watermelon	*Lasioglossum_callidum*	SD	0.01
Watermelon	*Lasioglossum_cattellae*	TD	0.00
Watermelon	*Lasioglossum_cinctipes*	SD	0.00
Watermelon	*Lasioglossum_coreopsis*	TD	0.00
Watermelon	*Lasioglossum_coriaceum*	SD	0.00
Watermelon	*Lasioglossum_cressonii*	SD	0.01
Watermelon	*Lasioglossum_ellisiae*	TD	0.01
Watermelon	*Lasioglossum_ephialtum*	SD	0.02
Watermelon	*Lasioglossum_georgeickworti*	SD	0.00
Watermelon	*Lasioglossum_gotham*	SD	0.00

Watermelon	*Lasioglossum_illinoense*	TD	0.05
Watermelon	*Lasioglossum_imitatum*	TD	0.59
Watermelon	*Lasioglossum_laevissimum*	SD	0.00
Watermelon	*Lasioglossum_leucocomum*	SD	0.02
Watermelon	*Lasioglossum_leucozonium*	LDS	0.09
Watermelon	*Lasioglossum_lineatulum*	SD	0.00
Watermelon	*Lasioglossum_mitchelli*	TD	0.17
Watermelon	*Lasioglossum_nymphaearum*	SD	0.04
Watermelon	*Lasioglossum_oblongum*	SD	0.01
Watermelon	*Lasioglossum_obscurum*	SD	0.01
Watermelon	*Lasioglossum_paradmirandum*	TD	0.04
Watermelon	*Lasioglossum_pectinatum*	SD	0.00
Watermelon	*Lasioglossum_pectorale*	SD	0.02
Watermelon	*Lasioglossum_pilosum*	SD	0.28
Watermelon	*Lasioglossum_planatum*	SD	0.00
Watermelon	*Lasioglossum_platyparium*	SD	0.00
Watermelon	*Lasioglossum_rozeni*	SD	0.00
Watermelon	*Lasioglossum_smilacinae*	SD	0.00
Watermelon	*Lasioglossum_subviridatum*	SD	0.00
Watermelon	*Lasioglossum_tegulare*	TD	0.07
Watermelon	*Lasioglossum_trigeminum*	SD	0.02
Watermelon	*Lasioglossum_truncatum*	SD	0.01
Watermelon	*Lasioglossum_versatum*	SD	0.44
Watermelon	*Lasioglossum_viridatum*	SD	0.01
Watermelon	*Lasioglossum_weemsi*	TD	0.05
Watermelon	*Lasioglossum_zephyrum*	SD	0.04
Watermelon	*Megachile_brevis*	LDS	0.06
Watermelon	*Megachile_mendica*	LDS	0.18
Watermelon	*Megachile_rotundata*	LDS	0.03
Watermelon	*Megachile_sculpturalis*	LDS	0.03
Watermelon	*Melissodes_bimaculata*	MEL	0.99
Watermelon	*Melissodes_trinodis*	MEL	0.00
Watermelon	*Nomada_articulata*	TRI	0.01
Watermelon	*Peponapis_pruinosa*	PEP	1.00
Watermelon	*Ptilothrix_bombiformis*	MEL	0.01
Watermelon	*Triepeolus_lunatus*	TRI	0.01
Watermelon	*Triepeolus_remigatus*	TRI	0.98
Watermelon	*Xylocopa_virginica*	XYL	1.00

Table A3: Response trait model estimates for all variables, including the fourth corner interactions. Note that many coefficients are set to zero due to

the lasso penalty which acts as model selection.

crop	variable	estimates
watermelon	Intercept	-0.576421649
watermelon	sppAgapostemon_sericeus	-0.009279838
watermelon	sppAgapostemon_texanus	-0.014124596
watermelon	sppAgapostemon_virescens	0
watermelon	sppAugochlora_pura	0.558159608
watermelon	sppAugochlorella_aurata	0.252162681
watermelon	sppAugochloropsis_metallica	-0.102126726
watermelon	sppBombus_bimaculatus	-0.068328543
watermelon	sppBombus_griseocollis	-0.044189731
watermelon	sppBombus_impatiens	0.725048904
watermelon	sppCalliopsis_andreniformis	-0.029828203
watermelon	sppCeratina_calcarata_dupla_miqmaki	0.280782801
watermelon	sppCeratina_strenua	0
watermelon	sppHalictus_confusus	0.18712962
watermelon	sppHalictus_ligatus	0.135271953
watermelon	sppHalictus_parallelus	-0.096935391
watermelon	sppHalictus_rubicundus	0
watermelon	sppLasioglossum_admirandum	-0.129706998
watermelon	sppLasioglossum_albipenne	-0.118065531
watermelon	sppLasioglossum_bruneri	0
watermelon	sppLasioglossum_coriaceum	-0.107890698
watermelon	sppLasioglossum_cressonii	-0.071238004
watermelon	sppLasioglossum_ephialtum	0
watermelon	sppLasioglossum_illinoense	0.036021268
watermelon	sppLasioglossum_imitatum	0.55394426
watermelon	sppLasioglossum_leucocomum	0.002812834

watermelon	sppLasioglossum_mitchelli	0.283412671
watermelon	sppLasioglossum_nymphaearum	0
watermelon	sppLasioglossum_oblongum	-0.118783972
watermelon	sppLasioglossum_obscurum	-0.07245479
watermelon	sppLasioglossum_paradmirandum	0.133974695
watermelon	sppLasioglossum_pectorale	0.041004684
watermelon	sppLasioglossum_pilosum	0.337276238
watermelon	sppLasioglossum_rozeni	-0.150752269
watermelon	sppLasioglossum_smilacinae	-0.106925589
watermelon	sppLasioglossum_tegulare	0.069406914
watermelon	sppLasioglossum_trigeminum	-0.021964911
watermelon	sppLasioglossum_truncatum	0
watermelon	sppLasioglossum_versatum	0.428595442
watermelon	sppLasioglossum_weemsi	0.203014094
watermelon	sppLasioglossum_zephyrum	0
watermelon	sppMegachile_mendica	-0.040327507
watermelon	sppMelissodes_bimaculata	0.338962415
watermelon	sppPeponapis_pruinosa	0.298377021
watermelon	sppTriepeolus_remigatus	0.142618209
watermelon	sppXylocopa_virginica	0
watermelon	agriculture_300	-0.033515551
watermelon	semi-natural_300	0.124754762
watermelon	agriculture_1500	-0.047821623
watermelon	semi-natural_1500	0.083440715
watermelon	agriculture_300.squ	-0.042700664
watermelon	semi-natural_300.squ	-0.055003683
watermelon	agriculture_1500.squ	-0.096777603
watermelon	semi-natural_1500.squ	0
watermelon	Nest_placecavity	0

watermelon	Nest_placehole	0
watermelon	Nest_placesoil	0
watermelon	Nest_placestem	0.198778917
watermelon	Nest_placewood	0
watermelon	SocialityEusocial	0
watermelon	Socialityfac_social	0
watermelon	SocialitySolitary	0
watermelon	ParasiticYes	0
watermelon	body_size	-0.173420908
watermelon	specialization	0
watermelon	tongue	0
watermelon	body_size.squ	0
watermelon	specialization.squ	0
watermelon	tongue.squ	0
watermelon	agriculture_300:Nest_placecavity	0
watermelon	agriculture_300:Nest_placehole	0
watermelon	agriculture_300:Nest_placesoil	0
watermelon	agriculture_300:Nest_placestem	-0.049978079
watermelon	agriculture_300:Nest_placewood	0
watermelon	agriculture_300:SocialityEusocial	0
watermelon	agriculture_300:Socialityfac_social	0
watermelon	agriculture_300:SocialitySolitary	0
watermelon	agriculture_300:ParasiticYes	0.108922029
watermelon	agriculture_300:body_size	0.192003954
watermelon	agriculture_300:specialization	0
watermelon	agriculture_300:tongue	0
watermelon	semi-natural_300:Nest_placecavity	0
watermelon	semi-natural_300:Nest_placehole	0
watermelon	semi-natural_300:Nest_placesoil	0.038326704

watermelon	semi-natural_300:Nest_placestem	0
watermelon	semi-natural_300:Nest_placewood	0
watermelon	semi-natural_300:SocialityEusocial	0.00808636
watermelon	semi-natural_300:Sociality fac_social	0
watermelon	semi-natural_300:SocialitySolitary	-0.013199001
watermelon	semi-natural_300:ParasiticYes	-0.039553688
watermelon	semi-natural_300:body_size	0
watermelon	semi-natural_300:specialization	0.061463166
watermelon	semi-natural_300:tongue	0
watermelon	agriculture_1500:Nest_placecavity	0
watermelon	agriculture_1500:Nest_placehole	0
watermelon	agriculture_1500:Nest_placesoil	-0.005213896
watermelon	agriculture_1500:Nest_placestem	0.017326634
watermelon	agriculture_1500:Nest_placewood	0
watermelon	agriculture_1500:SocialityEusocial	0
watermelon	agriculture_1500:Sociality fac_social	0
watermelon	agriculture_1500:SocialitySolitary	0
watermelon	agriculture_1500:ParasiticYes	0
watermelon	agriculture_1500:body_size	-0.063254087
watermelon	agriculture_1500:specialization	0.061183593
watermelon	agriculture_1500:tongue	0
watermelon	semi-natural_1500:Nest_placecavity	-0.036150993
watermelon	semi-natural_1500:Nest_placehole	-0.0710914
watermelon	semi-natural_1500:Nest_placesoil	0
watermelon	semi-natural_1500:Nest_placestem	0.056228857
watermelon	semi-natural_1500:Nest_placewood	0
watermelon	semi-natural_1500:SocialityEusocial	-0.010382428
watermelon	semi-natural_1500:Sociality fac_social	0
watermelon	semi-natural_1500:SocialitySolitary	0

watermelon	semi-natural_1500:ParasiticYes	0.134685819
watermelon	semi-natural_1500:body_size	0
watermelon	semi-natural_1500:specialization	-0.099793932
watermelon	semi-natural_1500:tongue	0
blueberry	Intercept	-1.105790242
blueberry	sppAndrena_bradleyi	0.42049863
blueberry	sppAndrena_cressonii	0
blueberry	sppAndrena_fenningeri	0
blueberry	sppAndrena_morrisonella	0
blueberry	sppAndrena_vicina	0.019815503
blueberry	sppAugochlora_pura	0
blueberry	sppAugochlorella_aurata	0
blueberry	sppBombus_bimaculatus	0
blueberry	sppBombus_griseocollis	0
blueberry	sppBombus_impatiens	0
blueberry	sppBombus_perplexus	0
blueberry	sppColletes_inaequalis	0.126105594
blueberry	sppColletes_thoracicus	0
blueberry	sppColletes_validus	0.083273954
blueberry	sppHabropoda_laboriosa	0
blueberry	sppLasioglossum_leucocomum	0
blueberry	sppLasioglossum_oblongum	0
blueberry	sppLasioglossum_pilosum	0
blueberry	sppLasioglossum_versatum	0
blueberry	sppLasioglossum_weemsi	0
blueberry	sppOsmia_pumila	0
blueberry	sppXylocopa_virginica	0
blueberry	agriculture_300	-0.26658714
blueberry	semi-natural_300	0

blueberry	agriculture_1500	-0.115548638
blueberry	semi-natural_1500	0
blueberry	agriculture_300.squ	0.177220016
blueberry	semi-natural_300.squ	0
blueberry	agriculture_1500.squ	0
blueberry	semi-natural_1500.squ	0
blueberry	Nest_placecavity	0
blueberry	Nest_placehole	0
blueberry	Nest_placesoil	0
blueberry	Nest_placewood	0
blueberry	SocialityEusocial	0
blueberry	Socialityfac_social	0
blueberry	SocialitySolitary	0
blueberry	body_size	0.569257497
blueberry	specialization	0
blueberry	tongue	0
blueberry	body_size.squ	0
blueberry	specialization.squ	0.1567025
blueberry	tongue.squ	0
blueberry	agriculture_300:Nest_placecavity	0
blueberry	agriculture_300:Nest_placehole	0
blueberry	agriculture_300:Nest_placesoil	0
blueberry	agriculture_300:Nest_placewood	0
blueberry	agriculture_300:SocialityEusocial	0
blueberry	agriculture_300:Socialityfac_social	0
blueberry	agriculture_300:SocialitySolitary	0
blueberry	agriculture_300:body_size	0
blueberry	agriculture_300:specialization	0
blueberry	agriculture_300:tongue	0

blueberry	semi-natural_300:Nest_placecavity	0
blueberry	semi-natural_300:Nest_placehole	0
blueberry	semi-natural_300:Nest_placesoil	0
blueberry	semi-natural_300:Nest_placewood	0
blueberry	semi-natural_300:SocialityEusocial	0
blueberry	semi-natural_300:Socialityfac_social	0
blueberry	semi-natural_300:SocialitySolitary	0
blueberry	semi-natural_300:body_size	0
blueberry	semi-natural_300:specialization	0
blueberry	semi-natural_300:tongue	0
blueberry	agriculture_1500:Nest_placecavity	0
blueberry	agriculture_1500:Nest_placehole	0
blueberry	agriculture_1500:Nest_placesoil	0
blueberry	agriculture_1500:Nest_placewood	0
blueberry	agriculture_1500:SocialityEusocial	0
blueberry	agriculture_1500:Socialityfac_social	0
blueberry	agriculture_1500:SocialitySolitary	0
blueberry	agriculture_1500:body_size	-0.065424217
blueberry	agriculture_1500:specialization	0
blueberry	agriculture_1500:tongue	-0.30068745
blueberry	semi-natural_1500:Nest_placecavity	0
blueberry	semi-natural_1500:Nest_placehole	0
blueberry	semi-natural_1500:Nest_placesoil	0
blueberry	semi-natural_1500:Nest_placewood	0
blueberry	semi-natural_1500:SocialityEusocial	0
blueberry	semi-natural_1500:Socialityfac_social	0
blueberry	semi-natural_1500:SocialitySolitary	0
blueberry	semi-natural_1500:body_size	0
blueberry	semi-natural_1500:specialization	0

blueberry	semi-natural_1500:tongue	0
cranberry	Intercept	-0.631992954
cranberry	sppAgapostemon_splendens	0
cranberry	sppAndrena_imitatrix	-0.040613799
cranberry	sppAndrena_vicina	0
cranberry	sppAugochlora_pura	0
cranberry	sppAugochlorella_aurata	0.352482114
cranberry	sppAugochloropsis_metallica	0.236752572
cranberry	sppAugochloropsis_sumptuosa	0.121551536
cranberry	sppBombus_bimaculatus	0.080454703
cranberry	sppBombus_griseocollis	0.084130022
cranberry	sppBombus_impatiens	0.164000021
cranberry	sppBombus_perplexus	0
cranberry	sppBombus_vagans	-0.086979307
cranberry	sppCeratina_calcarata_dupla_miqmaki	0
cranberry	sppCoelioxys_immaculata	0
cranberry	sppCoelioxys_porterae	0
cranberry	sppHeriades_carinatus	0
cranberry	sppHoplitis_truncata	0
cranberry	sppHylaeus_affinis	0.046287451
cranberry	sppLasioglossum_apopkense	-0.015975843
cranberry	sppLasioglossum_creberrimum	0
cranberry	sppLasioglossum_fuscipenne	0
cranberry	sppLasioglossum_georgeickworti	0.103453894
cranberry	sppLasioglossum_lineatulum	0
cranberry	sppLasioglossum_oblongum	0.065553692
cranberry	sppLasioglossum_pilosum	0
cranberry	sppLasioglossum_subviridatum	0.103315494
cranberry	sppLasioglossum_trigeminum	0

cranberry	sppLasioglossum_versatum	0
cranberry	sppMegachile_addenda	0
cranberry	sppMegachile_gemula	0
cranberry	sppMegachile_mendica	0
cranberry	sppMegachile_texana	0
cranberry	sppMelitta_americana	0.371484288
cranberry	sppNomada_rodecki	0.28043488
cranberry	sppOsmia_inspergens	0
cranberry	sppOsmia_pumila	0
cranberry	sppOsmia_virga	0.24124345
cranberry	sppPanurginus_atramontensis	0
cranberry	sppSphecodes_aroniae	0
cranberry	sppSphecodes_fattigi	0
cranberry	sppXylocopa_virginica	0
cranberry	agriculture_300	0
cranberry	semi-natural_300	0
cranberry	agriculture_1500	-0.239273032
cranberry	semi-natural_1500	0
cranberry	agriculture_300.squ	0
cranberry	semi-natural_300.squ	0
cranberry	agriculture_1500.squ	0
cranberry	semi-natural_1500.squ	0.161123069
cranberry	Nest_placecavity	0.788141301
cranberry	Nest_placehole	0
cranberry	Nest_placesoil	0
cranberry	Nest_placestem	0
cranberry	Nest_placewood	0.210443302
cranberry	SocialityEusocial	0.119359227
cranberry	Socialityfac_social	0

cranberry	SocialitySolitary	0
cranberry	ParasiticYes	-0.002756197
cranberry	body_size	0.360722617
cranberry	specialization	0
cranberry	tongue	0
cranberry	body_size.squ	0
cranberry	specialization.squ	0.278531163
cranberry	tongue.squ	0.236448892
cranberry	agriculture_300:Nest_placecavity	-0.041561834
cranberry	agriculture_300:Nest_placehole	0
cranberry	agriculture_300:Nest_placesoil	0
cranberry	agriculture_300:Nest_placestem	0
cranberry	agriculture_300:Nest_placewood	0
cranberry	agriculture_300:SocialityEusocial	0
cranberry	agriculture_300:Socialityfac_social	0
cranberry	agriculture_300:SocialitySolitary	-0.063994245
cranberry	agriculture_300:ParasiticYes	0
cranberry	agriculture_300:body_size	0
cranberry	agriculture_300:specialization	0.038303398
cranberry	agriculture_300:tongue	0
cranberry	semi-natural_300:Nest_placecavity	-0.052194922
cranberry	semi-natural_300:Nest_placehole	0
cranberry	semi-natural_300:Nest_placesoil	0
cranberry	semi-natural_300:Nest_placestem	0
cranberry	semi-natural_300:Nest_placewood	0.139451554
cranberry	semi-natural_300:SocialityEusocial	0
cranberry	semi-natural_300:Socialityfac_social	0
cranberry	semi-natural_300:SocialitySolitary	0
cranberry	semi-natural_300:ParasiticYes	0

cranberry	semi-natural_300:body_size	0
cranberry	semi-natural_300:specialization	0.111563737
cranberry	semi-natural_300:tongue	0
cranberry	agriculture_1500:Nest_placecavity	-0.016970912
cranberry	agriculture_1500:Nest_placehole	0
cranberry	agriculture_1500:Nest_placesoil	0
cranberry	agriculture_1500:Nest_placestem	0
cranberry	agriculture_1500:Nest_placewood	0
cranberry	agriculture_1500:SocialityEusocial	0
cranberry	agriculture_1500:Socialityfac_social	0
cranberry	agriculture_1500:SocialitySolitary	0
cranberry	agriculture_1500:ParasiticYes	0
cranberry	agriculture_1500:body_size	0.053019912
cranberry	agriculture_1500:specialization	0
cranberry	agriculture_1500:tongue	0
cranberry	semi-natural_1500:Nest_placecavity	0
cranberry	semi-natural_1500:Nest_placehole	0
cranberry	semi-natural_1500:Nest_placesoil	0.150882962
cranberry	semi-natural_1500:Nest_placestem	0
cranberry	semi-natural_1500:Nest_placewood	0
cranberry	semi-natural_1500:SocialityEusocial	0
cranberry	semi-natural_1500:Socialityfac_social	0
cranberry	semi-natural_1500:SocialitySolitary	0
cranberry	semi-natural_1500:ParasiticYes	0
cranberry	semi-natural_1500:body_size	0.093262373
cranberry	semi-natural_1500:specialization	0
cranberry	semi-natural_1500:tongue	0

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712 values.

Crop	Measure	Model	Delta AICc
Watermelon	Visitation Frequency	~ body size + tongue	0
Watermelon	Visitation Frequency	~ tongue	0.06
Watermelon	Visitation Frequency	~ .	0.28
Watermelon	Visitation Frequency	~ body size	1.99
Watermelon	Pollen deposition	~ body size + tongue	0
Cranberry	Visitation Frequency	~ sociality + tongue	0
Cranberry	Visitation Frequency	~ nest place	1.43
Cranberry	Visitation Frequency	~ sociality	1.56
Cranberry	Pollen deposition	~ .	0
Blueberry	Visitation Frequency	~ specialization	0
Blueberry	Pollen deposition	~ tongue	0

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