

1 **Pollinator species traits do not predict either response to**
2 **agricultural intensification or functional contribution**

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10 **Running headline:** Pollinator traits are not predictive

11 **Summary:**

12 1. The response and effect trait framework, if supported empirically, would
13 provide for powerful and general predictions about how biodiversity loss will
14 lead to loss in ecosystem function.

15 2. This framework proposes that species traits will explain how different
16 species respond to disturbance (i.e. response traits) as well as their
17 contribution to ecosystem function (i.e. effect traits). However, predictive
18 response and effect traits remain elusive for most systems.

19 3. Here, we present detailed data on crop pollination services provided by
20 native, wild bees to explore the role of six commonly used species traits in
21 determining how crop pollination is affected by increasing agricultural
22 intensification. Analyses were conducted in parallel for three crop systems
23 (watermelon, cranberry, and blueberry) located within the same geographical
24 region (mid-Atlantic USA).

25 4. Bee species traits did not strongly predict species' response to any
26 agricultural intensification process, and the few traits that were weakly
27 predictive were not consistent across crops. Similarly, no trait predicted
28 species' overall functional contribution in any of the three crop systems,
29 although body size was a good predictor of per capita efficiency in two
30 systems.

31 5. Pollinator traits may be useful for understanding ecological processes in
32 some systems, but thus far we are unable to make generalizable predictions
33 regarding species responses to land-use change and its effect on the delivery

34 of ecosystem services.

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

37

38 **Introduction**

39 Land-use change, along with other human-induced global change drivers, is
40 accelerating the rates of extinction of most taxa (Ellis et al. 2010). At the same
41 time, humanity relies on ecosystem services that wild species deliver, such as
42 pollination and pest control by insects, and nutrient cycling by microorganisms
43 (Cardinale *et al.* 2012). Thus, it is important to understand the relationship
44 between biodiversity loss and ecosystem service delivery (Schwartz et al.
45 2000). In particular, making generalizable predictions regarding how the
46 decline or local extinction of taxa will affect ecosystem services will allow for
47 targeted conservation actions to ameliorate negative impacts of land-use
48 change.

49 One avenue for predicting the functional consequences of biodiversity loss is
50 the response and effect trait framework (Lavorel & Garnier 2002, Naeem &
51 Wright 2003, McGill et al. 2006). Local extinction does not occur at random
52 because extinction risk is dependent on the species' characteristics.

53 Identifying which traits govern species responses to particular threats
54 ('response traits') would provide the first step for predicting future species
55 loss. Furthermore, the magnitude by which ecosystem function declines when

56 a species is lost depends on that species' functional contribution. This, too, is
57 likely to be mediated by the species' traits ('effect traits'). Therefore, the
58 relationship between response and effect traits will mediate the magnitude of
59 the impact of human disturbance on ecosystem services (Schleuning, Fründ &
60 García 2015). For example, if the same species traits that are associated with
61 high function are also most sensitive to disturbance, ecosystem function
62 would be predicted to decline rapidly (Larsen, Williams & Kremen 2005).

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

77 Here, we seek to identify response and effect traits for wild bee species
78 providing a key ecosystem service, crop pollination. The yield of most crop

79 plants increases with animal pollination (Klein *et al.* 2007). While managed
80 honey bees are a leading crop pollinator, wild insects contribute more than
81 half of pollinator visits to crop flowers across more than 40 crop systems
82 worldwide (Rader *et al.* 2016). A major threat to pollinators is habitat
83 destruction, primarily conversion to agriculture (Garibaldi *et al.* 2011), which is
84 also a leading cause of species loss worldwide (Pereira *et al.* 2010). Thus
85 agricultural land use has the potential to affect the ecosystem service upon
86 which agriculture itself depends (Deguines *et al.* 2014).

87 Our data sets were collected and analyzed in parallel and come from three
88 crop systems (watermelon, cranberry and blueberry) located within the same
89 geographical region (mid-Atlantic USA), but pollinated by distinct bee
90 communities. We determined whether six commonly-used species traits can
91 predict 1) species' responses to agricultural intensification (response traits)
92 and/or 2) species' contributions to crop pollination (effect traits).

93 **Material and methods:**

94 *Study system*

95 We selected 49 sites across three study systems that were located throughout
96 New Jersey and eastern Pennsylvania (USA). Watermelon sites (N = 17)
97 were located in 90 x 60 km region central New Jersey and Eastern
98 Pennsylvania, where the main types of land use are agriculture and suburban
99 development, interspersed with highly fragmented deciduous forest.
100 Cranberry and blueberry sites (N = 16 each) were both located within a 35 x

101 55 km area in southern New Jersey, where the main land cover types are
102 pine-oak ericaceous heath and agriculture. All sites in all systems were
103 separated by at least 1 km (range, watermelon: 2-90 km, cranberry: 1-32 km,
104 blueberry 1-38 km).

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

113 *Data collection:*

114 At all sites on all three crops, we used hand-netting to measure overall bee
115 abundance and species richness. To collect bees, we walked along fixed
116 transects at standard times of day and collected all bees observed to be
117 visiting flowers. In watermelon and blueberry, bees were netted three times
118 throughout the day for 20 minutes per transect (60 minutes per date per site)
119 and twice each day in cranberry for 30 minutes per transect (120 minutes per
120 date per site). Data were collected during the peak bloom in 2010
121 (watermelon: July, cranberry: late-May-early July, blueberry: April-early May).
122 Data were collected on three days per site for watermelon and blueberry and
123 two days per site for cranberry. Detailed methods can be found in Benjamin

124 Reilly & Winfree (2014), Winfree *et al.* (2015), Cariveau *et al.* (2013).

125 *Land cover characteristics of sites*

126 To relate pollinator response traits to land use, we required high-quality land
127 cover data for each pollinator collection site. For the cranberry and blueberry
128 sites in New Jersey, we used a continuous polygon layer classified by visual
129 photograph interpretation into 60 categories, at a minimum mapping unit of
130 4047 m² (1 acre; GIS Data provided by the New Jersey Department of
131 Environmental Protection). For watermelon sites that extend from central New
132 Jersey into Pennsylvania, we created a similar land cover data layer by
133 manually digitizing Google Earth imagery and visually classifying 15
134 categories, at a minimum mapping unit of 5,000 m² (1.24 acres). As each crop
135 was analyzed separately, our results are robust to using different land cover
136 data. However, to simplify the interpretation of results for the three crops, we
137 reclassified all land cover data into the following 7 broad categories:
138 agriculture, open managed (for example, mowed grass), open natural or semi-
139 natural (for example, old fields), semi-urban (<30% impervious surface), urban
140 (>30% impervious surface), wooded, and open water.

141 Prior to doing our spatial analyses, we explored several different landscape
142 characteristics, because agricultural land-use change can occur at multiple
143 scales and affect multiple landscape attributes. For each data collection site
144 we calculated four land cover variables: a) percent agriculture, b) percent
145 natural and semi-natural open habitat, c) forest edge length, and d) habitat
146 heterogeneity. We used agricultural land cover as our primary land use

147 change variable, as it is the dominant anthropogenic habitat type in all three
148 study systems. Percent open natural/semi-natural habitat makes up a small
149 proportion of the total land cover (mean 6.8% cover at 1500 m radius) but is
150 likely to be disproportionately important as forage and nesting habitat for bees
151 (Kleijn *et al.* 2006). Forest edge length may represent important habitat for
152 bees that nest in woods but forage in open areas (Kells & Goulson 2003).
153 Diverse patchy landscapes may be beneficial to bees as they may nest and
154 forage in different habitats (Kremen *et al.* 2007); thus we include Shannon H
155 diversity of the seven cover categories as a measure of habitat heterogeneity.
156 We calculated values for all four land cover variables at both a small scale
157 (300 m radius) and a large scale (1500 m radius), which correspond to typical
158 flight distances of small- and large-bodied bees, respectively (Greenleaf *et al.*
159 2007).

160 *Pollinator function*

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

167 To measure the pollination efficiency we quantified single-visit pollen
168 deposition by presenting virgin flowers to individual bees foraging on the
169 target crop. After visitation, we counted the number of pollen grains deposited

170 per flower visit (watermelon) or the number of pollen tetrads with pollen tubes
171 per flower visit (cranberry and blueberry). Because species identification in the
172 field is not possible for most bees and net collecting immediately after visits is
173 generally not possible, for the measurement of pollination efficiency we
174 grouped bees in species groups. Each group consisted of between one and
175 27 species, with the median number of species per group being 4 species
176 (Supporting Information, Table S1). Control flowers were left bagged until the
177 end of the field day, and contained few pollen grains (watermelon mean = 3
178 grains, N = 40 stigmas; cranberry mean = 0 tetrads, N = 82 stigmas; blueberry
179 mean = 2 tetrads, N= 734 stigmas). For detailed methods see Benjamin *et al.*
180 (2014), Winfree *et al.* (2015), Cariveau *et al.* (2013).

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 \pm 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 (Supporting Information. Text S2). Prior to calculating diet
210 breadth, we 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.

219 To calculate diet breadth for each bee species, we considered the number of
220 plants species as well as the phylogenetic breadth that the bees fed upon by
221 using a rarefied phylogenetic diversity index(Nipperess & Matsen 2013). To
222 determine phylogenetic distances among plants, we first constructed a
223 general phylogenetic tree using the PHYLOMATIC “megatree” (version
224 R201120829, Chamberlain & Szocs 2013) which defines relationships
225 between higher plants (Webb, Ackerly & Kembel 2008). We then dated nodes
226 across this tree according to Wikström et al. (2001) and used the branch-
227 length adjustment algorithm BLADJ to estimate the age of all remaining,
228 undated nodes. Though this procedure implies that ages within our
229 phylogenies should be treated as approximations (Beaulieu *et al.* 2007),
230 previous analysis indicates marked improvements of phylogenetic analyses
231 when even a limited number of nodes are properly dated (Webb 2000).

232 *Statistical analysis*

233 **Response traits:** In order to investigate which traits are associated with
234 environmental variables related to agricultural intensification, we used fourth-
235 corner analysis (Legendre Galzin & Harmelin-Vivien 1997). This analysis is
236 specifically designed to directly analyze the relationship between the
237 biological characteristics of species and the characteristics of the habitat
238 where they are found.

239 The fourth-corner approach links an R matrix of environmental variables to a

240 Q matrix of species traits through an L matrix of species abundance (Dray &
241 Legendre 2008). A correlation coefficient is computed for each pair of species
242 traits and environmental variables. We tested the significance of the trait-
243 environment correlation by combining two permutation models (Dray &
244 Legendre 2008). The first permutation randomizes site rows (or equivalently,
245 environmental variables across sites) to test if communities in different
246 environments have different trait values. The second permutation randomizes
247 species columns (or equivalently, trait values across species) to test if trait-
248 environment relationships are independent of community composition (Dray &
249 Legendre 2008). Under the second null model, a consistent trait-environment
250 relationship will not be significant if communities in similar environments have
251 similar species composition. Thus even if the first permutation is significant
252 but the second is not, we cannot know if the observed trait-environment
253 correlation simply reflects random changes in trait values due to the shift in
254 species composition. Hence, as recommended by Dray & Legendre (2008),
255 we report the highest p-value of the two models. We then ran the fourth-corner
256 analysis for each crop independently using 9999 permutations for each null
257 model (R package “ade4”; Dray & Dufour 2007). No adjustments for p-values
258 were made, but due to the high number of tests performed in the analyses,
259 the possibility of significance by chance increases. Therefore, we mainly
260 discuss effect sizes and only highlight results with significance level ≤ 0.01 ,
261 while we consider $0.01 > \alpha \leq 0.05$ to be relatively weakly supported
262 associations.

263 **Effect trait analysis:** To determine which traits influenced functional

264 contribution of each species we ran separate generalized linear models with
265 either visitation or per capita efficiency as response variables. Species traits
266 were predictors. The best model based on AICc was selected. When
267 differences between the best models were less than 2 we selected the simpler
268 model. The analysis for efficiency was done at the species group level (see
269 above: pollination function section). In order to obtain traits at the species
270 group level we calculated the mean values over species belonging to the
271 same group, weighted by the species mean abundance within the group. For
272 categorical variables we chose the dominant level.

273 All statistical analyses were performed in R software, version 3.0.3 (R Core
274 Team 2014).

275 **Results**

276 **Response traits:** Overall, we did not find a strong correlation between any
277 ecological traits and the environmental variables analyzed. Some traits
278 exhibited weak responses but they were not consistent across crops. For
279 watermelon, small bees and those with short tongues tended to decline with
280 increasing percentage of agriculture at 300m radius (Body size: $r = 0.23$, $p =$
281 0.03 , Tongue length: $r = 0.23$, $p = 0.03$). Species nesting in stems were
282 positively associated with heterogeneous landscapes at 1500m radius (Stem
283 nesters: $r = 0.12$, $p = 0.04$). For cranberry and blueberry, we did not find any
284 trait significantly associated with any of the landscape characteristics. A
285 complete list of all comparisons is presented in Supporting Information (Table
286 S3).

287 **Effect traits:** As for response traits, no traits were highly predictive of either
288 visitation frequency or per visit efficiency across crops. For watermelon, no
289 trait was selected on the best model for visitation frequency. However,
290 pollination efficiency was positively correlated with body size and tongue
291 length ($R^2 = 0.75$, $F_{2,9} = 17.07$, $p < 0.001$, Fig 2A). For cranberry, visitation
292 frequency was positively related to cavity nesters ($R^2 = 0.38$, $F_{4,36} = 7.1$, $p <$
293 0.0001 , Fig 2B). This result was driven by *Bombus* species, which are the only
294 cavity nesters in this data set. In contrast, efficiency per visit was not related
295 to any trait. For blueberry, visitation frequency was positively related to diet
296 specialism ($R^2 = 0.37$, $F_{1,20} = 13.5$, $p = 0.001$, Fig 2C), while efficiency per
297 visit is positively related to tongue length ($R^2 = 0.70$, $F_{1,5} = 14.9$, $p = 0.01$,
298 Fig 2D). Model selection, can be found in Supporting Information (Table S4).

299 **Discussion:**

300 Identifying traits that characterize which species are more sensitive to land-
301 use change or those that are functionally important is complex. We found
302 evidence for response and effect traits but they differed among crop species
303 as well as landscape variable used. Therefore, while some traits may be
304 important in some contexts, no traits were generalizable enough to be used to
305 predict how land-use change will influence the delivery of pollination services
306 in other systems. Further, the relationships identified were weak, especially for
307 response traits. This does not negate the importance of traits for
308 understanding which mechanisms underlie species responses to land use
309 change or pollination effectiveness, but it does suggest the commonly used

310 traits we studied here are not suitable for predictive purposes.

311 Being able to identify strong response traits would be a key tool for
312 understanding extinction risk, and an asset for conservation planning.

313 However, characterizing extinction risk based on traits is challenging. Despite
314 some generalities that emerge across taxa, with rare species, big species,
315 specialists, and higher trophic levels being in general more sensitive to
316 disturbances (Fisher & Owens 2004), there is a large variation in the response
317 of the species with those traits (Fritz, Bininda-Emonds & Purvis 2009; Seguin
318 *et al.* 2014). Work specifically on native bees has found that traits such as
319 specialization, body size, and sociality may predict responses to land use
320 (Winfree *et al.* 2009; Bommarco *et al.* 2010; Williams *et al.* 2010; Bartomeus
321 *et al.* 2013b; De Palma *et al.* 2015). However, studies often find contrasting
322 results. For example, De Palma *et al.* (2015) analyzed over 70,000 wild bee
323 records and found that small species were most sensitive to agricultural land
324 use, while others have found that larger species are more sensitive to
325 agricultural land use and/or environmental change generally (Larsen, Williams
326 & Kremen 2005; Bartomeus *et al.* 2013b; Rader *et al.* 2014), and some have
327 found little effect of body size (Williams *et al.* 2010). Here, we only found a
328 weak trend for big species to be more abundant in locally intense agricultural
329 areas in watermelon, but this trend disappears when land use is measured at
330 larger scales. Another trait, dietary specialization, is one of the few traits that
331 has been generally linked to increased species sensitivity to environmental
332 change (Williams *et al.* 2010; Scheper *et al.* 2014; De Palma *et al.* 2015), but
333 here we found that floral specialist bees did not decline with intensifying

334 agriculture. If anything, specialization is positively associated with agricultural
335 intensification in the blueberry system (Table S3), largely because the most
336 abundant bee species in this system (*Andrena bradleyi*) is a specialist on the
337 blueberry genus *Vaccinium*. Specialist bees observed in crop systems are
338 likely to be specialized on the crop plant family as was the case in our data
339 (e.g. *Habropoda sp.*, *Andrena bradleyi* in blueberry, but also *Peoponapis sp.*
340 in watermelon and *Mellita americana* in cranberry). We would expect different
341 responses from study designs that include natural habitat and a larger range
342 of specialist host plants (Forrest et al. 2015, Bartomeus & Winfree 2013).

343 Effect traits have been even harder to identify for pollinators. The limited data
344 published on particular plants suggests insects with larger bodies tend to
345 deposit more pollen per flower visit, but this pollen was not well distributed on
346 the stigma (Hoehn *et al.* 2008), or that the correlation between body size and
347 per visit pollination function is low (Larsen, Williams & Kremen 2005). Our
348 study supports the positive correlation between body size and per-visit pollen
349 deposition in both watermelon and blueberry (although note that tongue
350 length is correlated with body size in blueberry $r = 0.76$), but not for cranberry.
351 Hence, generality is difficult to achieve because a single pollinator trait, like
352 big body size, may not lead to high pollination function in all contexts. Rather it
353 seems likely that the most efficient trait will depend on the crop (Garibaldi *et*
354 *al.* 2015). Moreover, the total pollination provided by a pollinator species is the
355 product of visitation frequency and per capita efficiency (Kremen *et al.* 2005),
356 two processes that may be governed by different traits.

357 If generalizable response and effect traits can be found, the final step will be
358 to link response and effects to predict changes in ecosystem services. A
359 positive association between the response and effect traits (Naeem & Wright
360 2003) such that species with the strongest response to environmental change
361 also had the strongest effect on function, indicates the land-use change has
362 the potential for dramatic effects on ecosystem function. Whether response
363 and effect traits are in general positively, negatively, or uncorrelated is an
364 important question that has not yet been answered (Larsen, Williams &
365 Kremen 2005). Despite the conceptual elegance of the response-effect trait
366 framework, it is only effective if it is predictive, and strong evidence for the
367 generality of traits has not yet been found. For example, even the very
368 thorough and rigorously analyzed study of response-effect relationships by
369 Larsen, Williams & Kremen (2005) is based on a non-significant weak
370 relationship between pollinator per visit efficiency and body size. In our study,
371 even the strongest correlations find for watermelon, where big species are
372 less sensitive to local agricultural intensification and more efficient per visit,
373 but not more frequent flower visitors than smaller species are too weak to be
374 useful for predictive purposes.

375 Predictive response and/or effect traits are often assumed in the larger
376 literature as well. For example, recent re-evaluations of community stability in
377 food webs shows that using body size as proxy of extinction risk changes the
378 outcome of the stability simulations (Brose *et al.* 2016). However, the
379 assumption that body size is a good predictor of extinction risk is not directly
380 validated. Given the correlation showing that bigger species are more

381 sensitive is usually weak (Fisher & Owens 2004), these kind of approaches
382 could produce misleading outcomes.

383 Currently trait data may be too coarse to reveal ubiquitous response and
384 effect traits for four reasons. First, some traits may simply reflect identity of
385 genera or higher taxonomic groups. For example, some bumble bee species
386 in our three systems (especially *B. impatiens*) are common, functionally
387 dominant, and robust to extinction (Cariveau *et al.* 2013, Winfree *et al.* 2015).
388 Some of the important response and effect traits that we found, such as cavity
389 nesting and body size, may simply be proxies for bumble bees. Bumble bee
390 species also share other traits (e.g. sociality) that are commonly used in trait
391 analyses. Therefore, studies that don't include phylogenetic correlations may
392 be simply characterizing the general relationship between disturbance and the
393 functionally dominant bumble bees, or other dominant taxa. As there is a great
394 variability in the responses to disturbance among bumble bee species
395 (Cameron *et al.* 2011; Bartomeus *et al.* 2013b, Persson *et al.* 2015) this may
396 also explain why some studies find big species to be more sensitive to land
397 use change (Larsen, Williams & Kremen 2005) and other studies find the
398 opposite (Rader *et al.* 2014, this study). Second, traits may interact in complex
399 ways and single traits may be not able to capture responses and functional
400 contributions across species (e.g. Bommarco *et al.* 2010, De Palma *et al.*
401 2015). Third, phenotypical variability within species, usually ignored in trait-
402 based approaches, may play a more important role than previously though
403 (Bolnik *et al.* 2011). Finally, the most important traits may not have been
404 studied. Response traits such as dispersal ability, fecundity, and nest

405 microclimate/soil type, and effect traits like floral visitation behavior or
406 hairiness may be better predictors than the traits we have now. However, if
407 these traits are not easy to measure across bee species, they may be of little
408 use. Traits databases that include an increasing number of traits and agreed-
409 upon measurement techniques similar to those used in plant ecology (Kattge
410 *et al.* 2011) but that are also open-access may lead to significant
411 advancements in functional trait ecology in wild bees.

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

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431 **Data Accessibility:** All data and code used in this manuscript is accessible in
432 github (https://github.com/ibartomeus/RE_traits) and will be archived on
433 acceptance in figshare.

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- 630

631 **Tables and Figures**

632 **Fig. 1: Relationships between traits and environmental variables for A)**

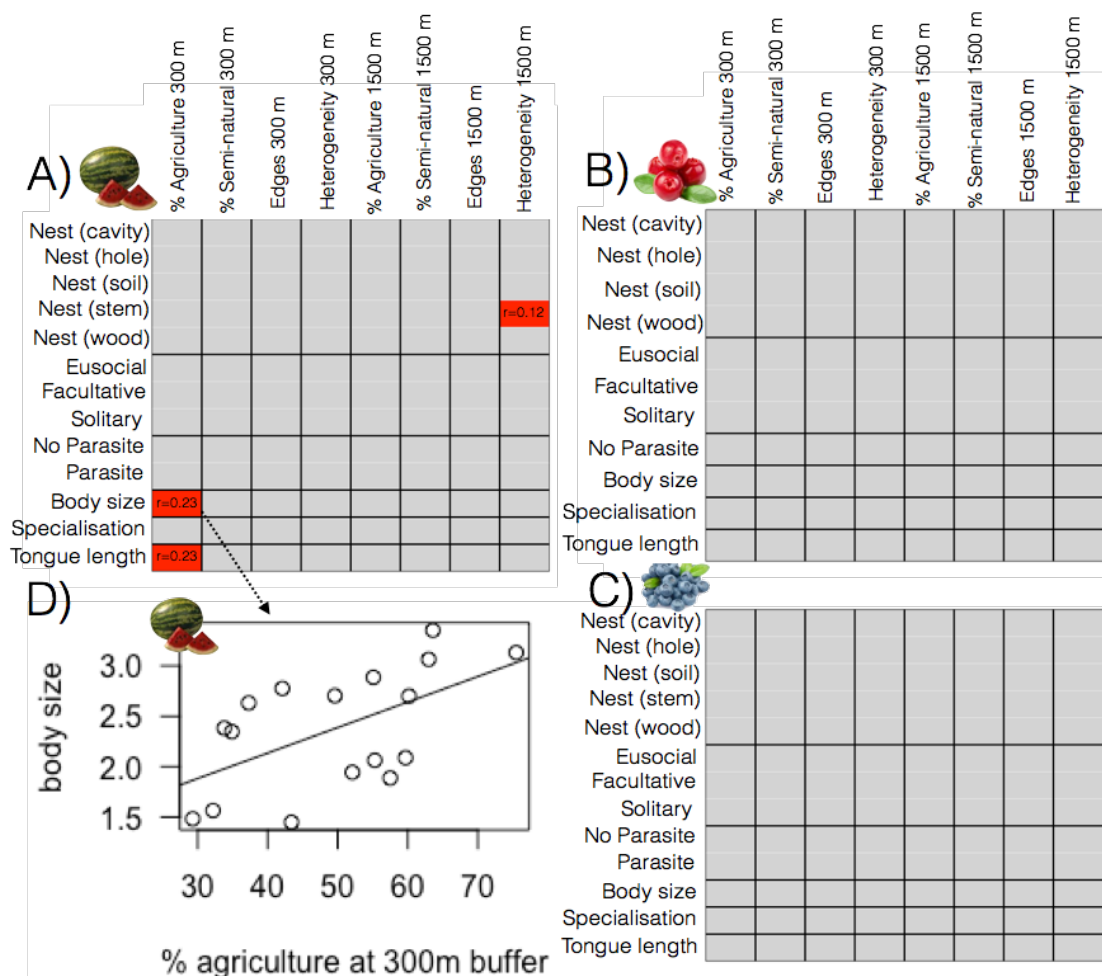
633 watermelon, B) blueberry and c) cranberry. Positive significant correlations

634 are in red ($p < 0.05$). Note no correlation is significant despite all the

635 combinations tested for both blueberry and cranberry. D) Detail of the

636 relationship between body size (visualized as the community weighted means

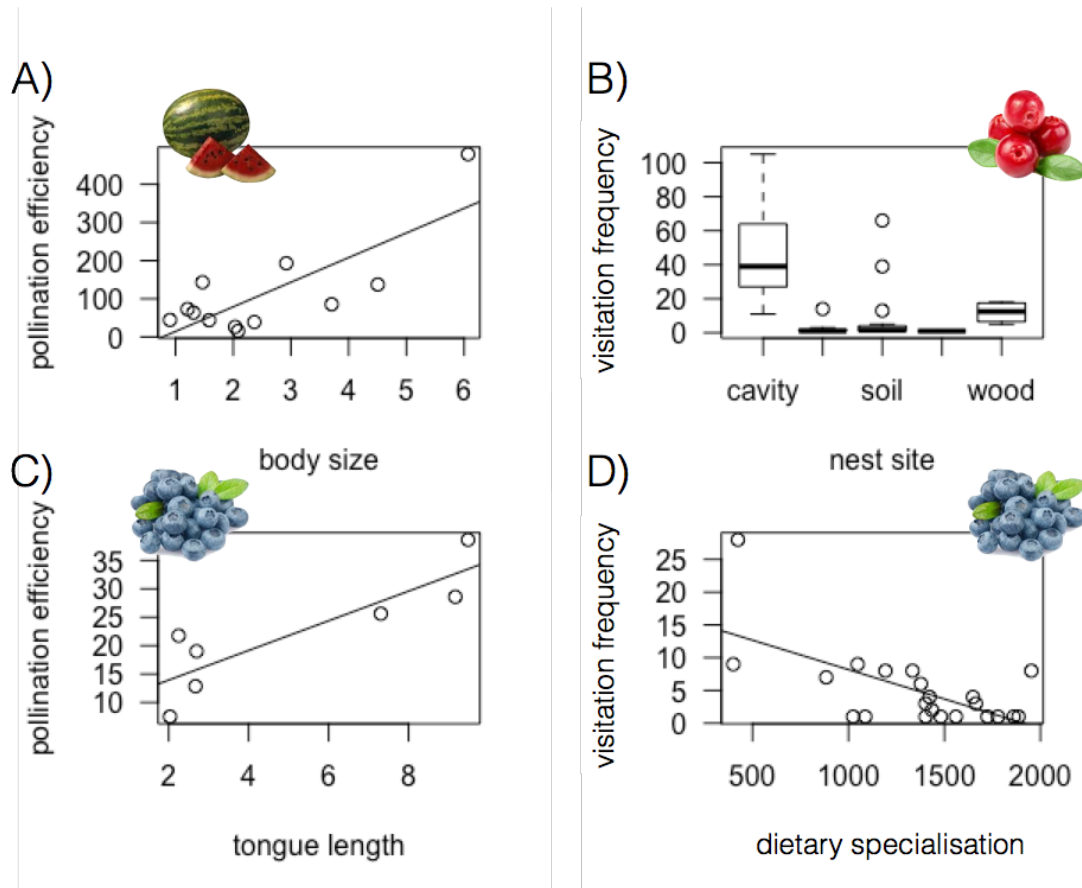
637 for each community) and percentage of agriculture at 300 meter radii.



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639

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



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645

646 Supporting Information

647 Table S1: Equivalencies between species and groups used for single visit

648 data.

Crop	Species	Single Visit Group	Percentage within group
Blueberry	<i>Andrena_banksi</i>	MED_AND	0.00
Blueberry	<i>Andrena_barbara</i>	MED_AND	0.00
Blueberry	<i>Andrena_bradleyi</i>	MED_AND	0.93
Blueberry	<i>Andrena_carlini</i>	LG_AND	0.12
Blueberry	<i>Andrena_carolina</i>	LG_AND	0.01
Blueberry	<i>Andrena_cressonii</i>	LG_AND	0.01
Blueberry	<i>Andrena_fenningeri</i>	MED_AND	0.01
Blueberry	<i>Andrena_hilaris</i>	MED_AND	0.00
Blueberry	<i>Andrena_ilicis</i>	MED_AND	0.00
Blueberry	<i>Andrena_imitatrix</i>	MED_AND	0.01
Blueberry	<i>Andrena_mandibularis</i>	MED_AND	0.00
Blueberry	<i>Andrena_morrisonella</i>	MED_AND	0.01
Blueberry	<i>Andrena_screpteroopsis</i>	MED_AND	0.00
Blueberry	<i>Andrena_vicina</i>	LG_AND	0.86
Blueberry	<i>Augochlora_pura</i>	Green	0.56
Blueberry	<i>Augochlorella_aurata</i>	Green	0.44
Blueberry	<i>Bombus_bimaculatus</i>	Bom_Q	0.24
Blueberry	<i>Bombus_griseocollis</i>	Bom_Q	0.49
Blueberry	<i>Bombus_impatiens</i>	Bom_Q	0.18
Blueberry	<i>Bombus_perplexus</i>	Bom_Q	0.08
Blueberry	<i>Ceratina_calcarata/dupla</i>	Dialictus	0.22
Blueberry	<i>Colletes_inaequalis</i>	Coll	0.26
Blueberry	<i>Colletes_thoracicus</i>	Coll	0.09
Blueberry	<i>Colletes_validus</i>	Coll	0.65
Blueberry	<i>Habropoda_laboriosa</i>	HAB	1.00
Blueberry	<i>Lasioglossum_acuminatum</i>	Dialictus	0.02
Blueberry	<i>Lasioglossum_coeruleum</i>	Dialictus	0.02
Blueberry	<i>Lasioglossum_fuscipenne</i>	Dialictus	0.02
Blueberry	<i>Lasioglossum_leucomum</i>	Dialictus	0.02
Blueberry	<i>Lasioglossum_oblongum</i>	Dialictus	0.10
Blueberry	<i>Lasioglossum_pilosum</i>	Dialictus	0.15
Blueberry	<i>Lasioglossum_versatum</i>	Dialictus	0.02
Blueberry	<i>Lasioglossum_weemsi</i>	Dialictus	0.07
Blueberry	<i>Lasioglossum_zephyrum</i>	Dialictus	0.05

Blueberry	<i>Nomada_luteola</i>	Dialictus	0.02
Blueberry	<i>Osmia_taurus</i>	Dialictus	0.02
Blueberry	<i>Osmia_cornifrons</i>	Dialictus	0.02
Blueberry	<i>Osmia_pumila</i>	Dialictus	0.07
Blueberry	<i>Sphecodes_aroniae</i>	Dialictus	0.02
Blueberry	<i>Sphecodes_stygius</i>	Dialictus	0.02
Blueberry	<i>Xylocopa_virginica</i>	XYL	1.00
Cranberry	<i>Agapostemon_splendens</i>	Green	0.02
Cranberry	<i>Andrena_cressonii</i>	Melitta	0.01
Cranberry	<i>Andrena_imitatrix</i>	Melitta	0.01
Cranberry	<i>Andrena_morrisonella</i>	Melitta	0.01
Cranberry	<i>Andrena_spiraeana</i>	Melitta	0.01
Cranberry	<i>Andrena_vicina</i>	Melitta	0.02
Cranberry	<i>Augochlora_pura</i>	Green	0.16
Cranberry	<i>Augochlorella_aurata</i>	Green	0.63
Cranberry	<i>Augochloropsis_metallica</i>	Green	0.16
Cranberry	<i>Augochloropsis_sumptuosa</i>	Green	0.03
Cranberry	<i>Bombus_bimaculatus</i>	<i>Bombus_bimaculatus</i>	1.00
Cranberry	<i>Bombus_citrinus</i>	<i>Bombus_spp</i>	0.50
Cranberry	<i>Bombus_griseocollis</i>	<i>Bombus_griseocollis</i>	1.00
Cranberry	<i>Bombus_impatiens</i>	<i>Bombus_impatiens</i>	1.00
Cranberry	<i>Bombus_perplexus</i>	<i>Bom_pervag</i>	0.85
Cranberry	<i>Bombus_sandersoni</i>	<i>Bombus_spp</i>	0.50
Cranberry	<i>Bombus_vagans</i>	<i>Bom_pervag</i>	0.15
Cranberry	<i>Ceratina_calcarata/dupla</i>	Small_black	0.12
Cranberry	<i>Coelioxys_immaculata</i>	Megachile	0.02
Cranberry	<i>Coelioxys_porterae</i>	Megachile	0.04
Cranberry	<i>Coelioxys_sayi</i>	Megachile	0.02
Cranberry	<i>Colletes_consors</i>	Megachile	0.02
Cranberry	<i>Halictus_rubicundus</i>	Small_black	0.02
Cranberry	<i>Heriades_carinatus</i>	<i>Osmia</i>	0.08
Cranberry	<i>Hoplitis_truncata</i>	<i>Osmia</i>	0.12
Cranberry	<i>Hylaeus_affinis</i>	Small_black	0.08
Cranberry	<i>Lasioglossum_apopkense</i>	Small_black	0.01
Cranberry	<i>Lasioglossum_coeruleum</i>	Small_black	0.01
Cranberry	<i>Lasioglossum_creberrimum</i>	Small_black	0.02
Cranberry	<i>Lasioglossum_fuscipenne</i>	Small_black	0.05
Cranberry	<i>Lasioglossum_georgeickworti</i>	Small_black	0.05
Cranberry	<i>Lasioglossum_lineatulum</i>	Small_black	0.01
Cranberry	<i>Lasioglossum_oblongum</i>	Small_black	0.15
Cranberry	<i>Lasioglossum_pilosum</i>	Small_black	0.02
Cranberry	<i>Lasioglossum_planatum</i>	Small_black	0.02
Cranberry	<i>Lasioglossum_subviridatum</i>	Small_black	0.17
Cranberry	<i>Lasioglossum_trigeminum</i>	Small_black	0.02

Cranberry	<i>Lasioglossum_versatum</i>	Small_black	0.04
Cranberry	<i>Megachile_addenda</i>	Megachile	0.22
Cranberry	<i>Megachile_gemula</i>	Megachile	0.32
Cranberry	<i>Megachile_mendica</i>	Megachile	0.28
Cranberry	<i>Megachile_texana</i>	Megachile	0.08
Cranberry	<i>Melitta_americana</i>	Melitta	0.95
Cranberry	<i>Nomada_bella/lepida</i>	Small_black	0.01
Cranberry	<i>Nomada_pygmaea</i>	Small_black	0.01
Cranberry	<i>Nomada_rodecki</i>	Small_black	0.07
Cranberry	<i>Osmia_inspergens</i>	Osmia	0.07
Cranberry	<i>Osmia_pumila</i>	Osmia	0.13
Cranberry	<i>Osmia_virga</i>	Osmia	0.60
Cranberry	<i>Panurginus_atramontensis</i>	Small_black	0.09
Cranberry	<i>Sphecodes_aroniae</i>	Small_black	0.03
Cranberry	<i>Sphecodes_fattigi</i>	Small_black	0.01
Cranberry	<i>Xylocopa_virginica</i>	XYL	1.00
Watermelon	<i>Agapostemon_sericeus</i>	LG	0.25
Watermelon	<i>Agapostemon_texanus</i>	LG	0.11
Watermelon	<i>Agapostemon_virescens</i>	LG	0.52
Watermelon	<i>Anthidium_oblongatum</i>	LDS	0.03
Watermelon	<i>Augochlora_pura</i>	SG	0.80
Watermelon	<i>Augochlorella_aurata</i>	SG	0.20
Watermelon	<i>Augochloropsis_metallica</i>	LG	0.11
Watermelon	<i>Bombus_bimaculatus</i>	BOM	0.01
Watermelon	<i>Bombus_fervidus</i>	BOM	0.00
Watermelon	<i>Bombus_griseocollis</i>	BOM	0.01
Watermelon	<i>Bombus_impatiens</i>	BOM	0.98
Watermelon	<i>Bombus_perplexus</i>	BOM	0.00
Watermelon	<i>Bombus_vagans</i>	BOM	0.00
Watermelon	<i>Calliopsis_andreniformis</i>	SD	0.03
Watermelon	<i>Ceratina_calcarata/dupla</i>	CER	0.81
Watermelon	<i>Ceratina_strenua</i>	CER	0.19
Watermelon	<i>Halictus_confusus</i>	HAL_MDS	0.83
Watermelon	<i>Halictus_ligatus</i>	HAL_MDS	0.16
Watermelon	<i>Halictus_parallelus</i>	LDS	0.03
Watermelon	<i>Halictus_rubicundus</i>	LDS	0.56
Watermelon	<i>Hoplitis_pilosifrons</i>	HAL_MDS	0.00
Watermelon	<i>Hoplitis_producta</i>	HAL_MDS	0.00
Watermelon	<i>Hylaeus_affinis</i>	TD	0.01
Watermelon	<i>Lasioglossum_admirandum</i>	SD	0.01
Watermelon	<i>Lasioglossum_albipenne</i>	SD	0.00
Watermelon	<i>Lasioglossum_atwoodi</i>	SD	0.00
Watermelon	<i>Lasioglossum_bruneri</i>	SD	0.01
Watermelon	<i>Lasioglossum_callidum</i>	SD	0.01

Watermelon	<i>Lasioglossum_cattellae</i>	TD	0.00
Watermelon	<i>Lasioglossum_cinctipes</i>	SD	0.00
Watermelon	<i>Lasioglossum_coreopsis</i>	TD	0.00
Watermelon	<i>Lasioglossum_coriaceum</i>	SD	0.00
Watermelon	<i>Lasioglossum_cressonii</i>	SD	0.01
Watermelon	<i>Lasioglossum_ellisiae</i>	TD	0.01
Watermelon	<i>Lasioglossum_ephialtum</i>	SD	0.02
Watermelon	<i>Lasioglossum_georgeickworti</i>	SD	0.00
Watermelon	<i>Lasioglossum_gotham</i>	SD	0.00
Watermelon	<i>Lasioglossum_illinoense</i>	TD	0.05
Watermelon	<i>Lasioglossum_imitatum</i>	TD	0.59
Watermelon	<i>Lasioglossum_laevissimum</i>	SD	0.00
Watermelon	<i>Lasioglossum_leucomomum</i>	SD	0.02
Watermelon	<i>Lasioglossum_leucozonium</i>	LDS	0.09
Watermelon	<i>Lasioglossum_lineatulum</i>	SD	0.00
Watermelon	<i>Lasioglossum_mitchelli</i>	TD	0.17
Watermelon	<i>Lasioglossum_nymphaearum</i>	SD	0.04
Watermelon	<i>Lasioglossum_oblongum</i>	SD	0.01
Watermelon	<i>Lasioglossum_obscurum</i>	SD	0.01
Watermelon	<i>Lasioglossum_paradmirandum</i>	TD	0.04
Watermelon	<i>Lasioglossum_pectinatum</i>	SD	0.00
Watermelon	<i>Lasioglossum_pectorale</i>	SD	0.02
Watermelon	<i>Lasioglossum_pilosum</i>	SD	0.28
Watermelon	<i>Lasioglossum_planatum</i>	SD	0.00
Watermelon	<i>Lasioglossum_platyparium</i>	SD	0.00
Watermelon	<i>Lasioglossum_rozeni</i>	SD	0.00
Watermelon	<i>Lasioglossum_smilacinae</i>	SD	0.00
Watermelon	<i>Lasioglossum_subviridatum</i>	SD	0.00
Watermelon	<i>Lasioglossum_tegulare</i>	TD	0.07
Watermelon	<i>Lasioglossum_trigeminum</i>	SD	0.02
Watermelon	<i>Lasioglossum_truncatum</i>	SD	0.01
Watermelon	<i>Lasioglossum_versatum</i>	SD	0.44
Watermelon	<i>Lasioglossum_viridatum</i>	SD	0.01
Watermelon	<i>Lasioglossum_weemsi</i>	TD	0.05
Watermelon	<i>Lasioglossum_zephyrum</i>	SD	0.04
Watermelon	<i>Megachile_brevis</i>	LDS	0.06
Watermelon	<i>Megachile_mendica</i>	LDS	0.18
Watermelon	<i>Megachile_rotundata</i>	LDS	0.03
Watermelon	<i>Megachile_sculpturalis</i>	LDS	0.03
Watermelon	<i>Melissodes_bimaculata</i>	MEL	0.99
Watermelon	<i>Melissodes_trinodis</i>	MEL	0.00
Watermelon	<i>Nomada_articulata</i>	TRI	0.01
Watermelon	<i>Peponapis_pruinosa</i>	PEP	1.00
Watermelon	<i>Ptilothrix_bombiformis</i>	MEL	0.01

Watermelon	<i>Triepeolus_lunatus</i>	TRI	0.01
Watermelon	<i>Triepeolus_remigatus</i>	TRI	0.98
Watermelon	<i>Xylocopa_virginica</i>	XYL	1.00

649

650 Text S2: Datasets used for calculating dietary specialization: Six datasets
651 were used to create the phylogenetic distance index. All data were collected in
652 the region of the crop study. Specimens were collected using a hand net and
653 the bee species and plant species were recorded. This resulted in a total of
654 18,733 bee x plant interactions for species that were also in the crop dataset.
655 The number of species, sites, and years of collection are as follows: 1) Pine
656 barrens in 2003: 280 bee x plant interactions. Habitat types were extensive
657 pine-oak forest (14 sites), forest fragments (14 sites), suburban back yards (7
658 sites), and agricultural field borders (5 sites) in New Jersey (Winfree et al.
659 2007). Bees were collected in temporally stratified sampling rounds between
660 April and September. 2) NJPA: 3906 bee x plant interactions. Data collected
661 on watermelon field margins at a total of 20 sites. Farm types included small-
662 scale mixed farming, both crops and field margins, both organic and low-
663 pesticide-input conventional. All bees were collected in three temporally
664 stratified sampling rounds in July, in each of 3 years. 3) NFWF 3906 bee x
665 plant interactions. Habitat types were old fields. Bees were collected in May
666 through Sept at 25 sites for two years. *Lasioglossum* species were not
667 included for this dataset due to recent changes in its taxonomy. 4) NSF 2006
668 666 bee x plant interactions. Habitat types were deciduous forest fragments
669 (13 sites), and suburban / urban yards (3 sites) and sites with extensive
670 forests with diverse wildflower communities (4 sites). All bees were collected

671 in sampling rounds between April and early June. 5) CIG 4600 bee x plant
 672 interactions. Site were comprised of old fields as well as pollinator
 673 enhancement sites. Bees using were collected using a hand net from a total of
 674 a total 18 sites in 2011-2013. For each bee specimen, the plant species was
 675 recorded. 6) Cape May 5858 bee x plant interactions. This study included only
 676 one site. The habitat was an old field that had been planted in 20 species of
 677 native perennial plants. Sampling took place over 3 years in sampling rounds
 678 that occurred in May through September.

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

681 Table S3: Fourth corner results showing correlations and p-values for each
 682 trait. Significant values in bold.

Crop	Test	r	Standard deviation	P-value
watermelon	ag_300 / Nest_.cavity	0.19	1.92	0.05
watermelon	open_300 / Nest_.cavity	-0.09	-0.83	0.43
watermelon	forest_edge_300 / Nest_.cavity	-0.05	-0.31	0.71
watermelon	shannonH_300 / Nest_.cavity	-0.09	-0.88	0.4
watermelon	ag_1500 / Nest_.cavity	-0.11	-1	0.33
watermelon	open_1500 / Nest_.cavity	-0.15	-1.4	0.18
watermelon	forest_edge_1500 / Nest_.cavity	-0.02	-0.2	0.86
watermelon	shannonH_1500 / Nest_.cavity	-0.06	-0.54	0.62
watermelon	ag_300 / Nest_.hole	0	0.07	0.93
watermelon	open_300 / Nest_.hole	-0.03	-0.85	0.32
watermelon	forest_edge_300 / Nest_.hole	-0.06	-0.76	0.34
watermelon	shannonH_300 / Nest_.hole	-0.03	-0.63	0.41
watermelon	ag_1500 / Nest_.hole	-0.03	-0.54	0.41
watermelon	open_1500 / Nest_.hole	-0.05	-0.94	0.22
watermelon	forest_edge_1500 / Nest_.hole	-0.03	-0.65	0.36
watermelon	shannonH_1500 / Nest_.hole	-0.08	-1.61	0.09
watermelon	ag_300 / Nest_.soil	-0.12	-1.2	0.27
watermelon	open_300 / Nest_.soil	0.11	1.16	0.27

watermelon	forest_edge_300 / Nest_.soil	0.01	-0.07	0.95
watermelon	shannonH_300 / Nest_.soil	0.07	0.81	0.45
watermelon	ag_1500 / Nest_.soil	0.04	0.46	0.66
watermelon	open_1500 / Nest_.soil	0.07	0.73	0.5
watermelon	forest_edge_1500 / Nest_.soil	-0.05	-0.53	0.63
watermelon	shannonH_1500 / Nest_.soil	0.02	0.23	0.85
watermelon	ag_300 / Nest_.stem	-0.08	-1	0.26
watermelon	open_300 / Nest_.stem	0.03	0.44	0.66
watermelon	forest_edge_300 / Nest_.stem	0.01	0.11	0.93
watermelon	shannonH_300 / Nest_.stem	0.09	1.38	0.18
watermelon	ag_1500 / Nest_.stem	0	0.05	0.96
watermelon	open_1500 / Nest_.stem	0.07	0.87	0.27
watermelon	forest_edge_1500 / Nest_.stem	0.01	0.25	0.78
watermelon	shannonH_1500 / Nest_.stem	0.12	2.01	0.04
watermelon	ag_300 / Nest_.wood	-0.03	-0.22	0.76
watermelon	open_300 / Nest_.wood	-0.06	-0.84	0.43
watermelon	forest_edge_300 / Nest_.wood	0.05	0.66	0.52
watermelon	shannonH_300 / Nest_.wood	-0.05	-0.66	0.54
watermelon	ag_1500 / Nest_.wood	0.08	1.04	0.3
watermelon	open_1500 / Nest_.wood	0.04	0.51	0.59
watermelon	forest_edge_1500 / Nest_.wood	0.09	1.37	0.17
watermelon	shannonH_1500 / Nest_.wood	-0.04	-0.58	0.57
watermelon	ag_300 / Socia.Eusocial	0.02	0.18	0.91
watermelon	open_300 / Socia.Eusocial	-0.01	-0.09	0.93
watermelon	forest_edge_300 / Socia.Eusocial	0.04	0.27	0.86
watermelon	shannonH_300 / Socia.Eusocial	0.08	0.79	0.48
watermelon	ag_1500 / Socia.Eusocial	-0.04	-0.36	0.74
watermelon	open_1500 / Socia.Eusocial	-0.16	-1.61	0.11
	forest_edge_1500 /			
watermelon	Socia.Eusocial	-0.06	-0.61	0.56
watermelon	shannonH_1500 / Socia.Eusocial	0.01	0.12	0.92
watermelon	ag_300 / Socia.fac_social	-0.07	-0.64	0.54
watermelon	open_300 / Socia.fac_social	0.03	0.45	0.72
	forest_edge_300 /			
watermelon	Socia.fac_social	-0.01	0.02	0.99
watermelon	shannonH_300 / Socia.fac_social	0.06	0.86	0.47
watermelon	ag_1500 / Socia.fac_social	-0.01	-0.15	0.86
watermelon	open_1500 / Socia.fac_social	0.07	0.73	0.47
	forest_edge_1500 /			
watermelon	Socia.fac_social	0	-0.02	0.99
	shannonH_1500 /			
watermelon	Socia.fac_social	0.09	1.52	0.13
watermelon	ag_300 / Socia.Solitary	0.03	0.31	0.79
watermelon	open_300 / Socia.Solitary	-0.01	-0.15	0.89
watermelon	forest_edge_300 / Socia.Solitary	-0.03	-0.16	0.86

watermelon	shannonH_300 / Socia.Solitary	-0.14	-1.46	0.14
watermelon	ag_1500 / Socia.Solitary	0.05	0.54	0.61
watermelon	open_1500 / Socia.Solitary	0.13	1.33	0.2
watermelon	forest_edge_1500 / Socia.Solitary	0.07	0.74	0.48
watermelon	shannonH_1500 / Socia.Solitary	-0.08	-0.83	0.44
watermelon	ag_300 / Paras.No	-0.1	-0.85	0.48
watermelon	open_300 / Paras.No	-0.02	-0.24	0.88
watermelon	forest_edge_300 / Paras.No	-0.02	-0.22	0.82
watermelon	shannonH_300 / Paras.No	0.18	1.67	0.08
watermelon	ag_1500 / Paras.No	0	0	1
watermelon	open_1500 / Paras.No	-0.22	-2.07	0.05
watermelon	forest_edge_1500 / Paras.No	-0.12	-1.13	0.23
watermelon	shannonH_1500 / Paras.No	0.06	0.57	0.59
watermelon	ag_300 / Paras.Yes	0.1	0.85	0.48
watermelon	open_300 / Paras.Yes	0.02	0.24	0.88
watermelon	forest_edge_300 / Paras.Yes	0.02	0.22	0.82
watermelon	shannonH_300 / Paras.Yes	-0.18	-1.67	0.08
watermelon	ag_1500 / Paras.Yes	0	0	1
watermelon	open_1500 / Paras.Yes	0.22	2.07	0.05
watermelon	forest_edge_1500 / Paras.Yes	0.12	1.13	0.23
watermelon	shannonH_1500 / Paras.Yes	-0.06	-0.57	0.59
watermelon	ag_300 / ITfam	0.23	2.19	0.02
watermelon	open_300 / ITfam	-0.07	-0.61	0.56
watermelon	forest_edge_300 / ITfam	-0.1	-0.82	0.41
watermelon	shannonH_300 / ITfam	-0.15	-1.39	0.18
watermelon	ag_1500 / ITfam	-0.13	-1.15	0.27
watermelon	open_1500 / ITfam	-0.1	-0.94	0.36
watermelon	forest_edge_1500 / ITfam	-0.03	-0.29	0.79
watermelon	shannonH_1500 / ITfam	-0.09	-0.78	0.45
watermelon	ag_300 / PDrar20	-0.08	-0.76	0.52
watermelon	open_300 / PDrar20	-0.04	-0.53	0.63
watermelon	forest_edge_300 / PDrar20	0.02	0.18	0.88
watermelon	shannonH_300 / PDrar20	0.08	1	0.35
watermelon	ag_1500 / PDrar20	0.05	0.51	0.7
watermelon	open_1500 / PDrar20	-0.13	-1.56	0.12
watermelon	forest_edge_1500 / PDrar20	-0.06	-0.7	0.52
watermelon	shannonH_1500 / PDrar20	0.02	0.22	0.86
watermelon	ag_300 / tongue	0.23	2.18	0.02
watermelon	open_300 / tongue	-0.07	-0.64	0.55
watermelon	forest_edge_300 / tongue	-0.09	-0.76	0.45
watermelon	shannonH_300 / tongue	-0.14	-1.38	0.19
watermelon	ag_1500 / tongue	-0.12	-1.11	0.29
watermelon	open_1500 / tongue	-0.1	-0.92	0.37
watermelon	forest_edge_1500 / tongue	-0.03	-0.26	0.82

watermelon	shannonH_1500 / tongue	-0.08	-0.73	0.48
cranberry	ag_300 / Nest_.cavity	0.1	1.09	0.3
cranberry	open_300 / Nest_.cavity	-0.15	-1.62	0.11
cranberry	forest_edge_300 / Nest_.cavity	0	0.05	0.97
cranberry	shannonH_300 / Nest_.cavity	-0.07	-0.71	0.51
cranberry	ag_1500 / Nest_.cavity	0.05	0.48	0.65
cranberry	open_1500 / Nest_.cavity	-0.08	-0.69	0.5
cranberry	forest_edge_1500 / Nest_.cavity	-0.07	-0.75	0.47
cranberry	shannonH_1500 / Nest_.cavity	0.04	0.38	0.72
cranberry	ag_300 / Nest_.hole	0.01	0.12	0.91
cranberry	open_300 / Nest_.hole	-0.05	-0.56	0.58
cranberry	forest_edge_300 / Nest_.hole	0.01	0.18	0.88
cranberry	shannonH_300 / Nest_.hole	-0.03	-0.56	0.58
cranberry	ag_1500 / Nest_.hole	-0.04	-0.43	0.68
cranberry	open_1500 / Nest_.hole	-0.08	-0.64	0.56
cranberry	forest_edge_1500 / Nest_.hole	-0.02	-0.22	0.87
cranberry	shannonH_1500 / Nest_.hole	-0.05	-0.51	0.61
cranberry	ag_300 / Nest_.soil	-0.09	-0.89	0.41
cranberry	open_300 / Nest_.soil	0.09	0.97	0.36
cranberry	forest_edge_300 / Nest_.soil	0	0.01	1
cranberry	shannonH_300 / Nest_.soil	0.09	0.81	0.45
cranberry	ag_1500 / Nest_.soil	-0.04	-0.33	0.76
cranberry	open_1500 / Nest_.soil	0.13	1.08	0.3
cranberry	forest_edge_1500 / Nest_.soil	0.09	0.87	0.41
cranberry	shannonH_1500 / Nest_.soil	-0.02	-0.17	0.91
cranberry	ag_300 / Nest_.stem	-0.03	-0.52	0.36
cranberry	open_300 / Nest_.stem	0.02	0.21	0.84
cranberry	forest_edge_300 / Nest_.stem	0	0.07	0.94
cranberry	shannonH_300 / Nest_.stem	0.02	0.32	0.56
cranberry	ag_1500 / Nest_.stem	-0.01	-0.11	0.9
cranberry	open_1500 / Nest_.stem	0.03	0.51	0.44
cranberry	forest_edge_1500 / Nest_.stem	0.02	0.36	0.61
cranberry	shannonH_1500 / Nest_.stem	0	0.05	0.92
cranberry	ag_300 / Nest_.wood	-0.05	-0.55	0.6
cranberry	open_300 / Nest_.wood	0.17	1.77	0.07
cranberry	forest_edge_300 / Nest_.wood	-0.02	-0.3	0.76
cranberry	shannonH_300 / Nest_.wood	0.01	0.1	0.93
cranberry	ag_1500 / Nest_.wood	0	0.05	0.96
cranberry	open_1500 / Nest_.wood	0	-0.04	0.97
cranberry	forest_edge_1500 / Nest_.wood	0	0	1
cranberry	shannonH_1500 / Nest_.wood	-0.01	-0.07	0.94
cranberry	ag_300 / Socia.Eusocial	0.02	0.28	0.82
cranberry	open_300 / Socia.Eusocial	0.03	0.19	0.88
cranberry	forest_edge_300 / Socia.Eusocial	0.01	0.09	0.93

cranberry	shannonH_300 / Socia.Eusocial	0.02	0.28	0.8
cranberry	ag_1500 / Socia.Eusocial	-0.01	-0.08	0.95
cranberry	open_1500 / Socia.Eusocial	0.02	0.18	0.88
cranberry	forest_edge_1500 / Socia.Eusocial	-0.01	-0.14	0.92
cranberry	shannonH_1500 / Socia.Eusocial	0.01	0.12	0.91
cranberry	ag_300 / Socia.fac_social	0.03	0.75	0.47
cranberry	open_300 / Socia.fac_social	0.04	0.29	0.77
cranberry	forest_edge_300 / Socia.fac_social	-0.05	-1.15	0.29
cranberry	shannonH_300 / Socia.fac_social	-0.04	-0.71	0.32
cranberry	ag_1500 / Socia.fac_social	0.04	0.71	0.47
cranberry	open_1500 / Socia.fac_social	0.01	0.23	0.77
cranberry	forest_edge_1500 / Socia.fac_social	0.01	0.22	0.81
cranberry	shannonH_1500 / Socia.fac_social	0.03	0.56	0.5
cranberry	ag_300 / Socia.Solitary	-0.03	-0.41	0.74
cranberry	open_300 / Socia.Solitary	-0.04	-0.37	0.72
cranberry	forest_edge_300 / Socia.Solitary	0.01	0.15	0.9
cranberry	shannonH_300 / Socia.Solitary	-0.01	-0.09	0.94
cranberry	ag_1500 / Socia.Solitary	0	-0.03	0.97
cranberry	open_1500 / Socia.Solitary	-0.03	-0.23	0.86
cranberry	forest_edge_1500 / Socia.Solitary	0.01	0.07	0.96
cranberry	shannonH_1500 / Socia.Solitary	-0.02	-0.32	0.79
cranberry	ag_300 / Paras.No	0	-0.01	1
cranberry	open_300 / Paras.No	0.01	0.16	0.87
cranberry	forest_edge_300 / Paras.No	0	-0.05	0.96
cranberry	shannonH_300 / Paras.No	0	0.01	0.97
cranberry	ag_1500 / Paras.No	0	0.04	0.97
cranberry	open_1500 / Paras.No	0.01	-0.05	0.96
cranberry	forest_edge_1500 / Paras.No	0.02	0.14	0.88
cranberry	shannonH_1500 / Paras.No	0.03	0.24	0.74
cranberry	ag_300 / Paras.Yes	0	0.01	1
cranberry	open_300 / Paras.Yes	-0.01	-0.16	0.87
cranberry	forest_edge_300 / Paras.Yes	0	0.05	0.96
cranberry	shannonH_300 / Paras.Yes	0	-0.01	0.97
cranberry	ag_1500 / Paras.Yes	0	-0.04	0.97
cranberry	open_1500 / Paras.Yes	-0.01	0.05	0.96
cranberry	forest_edge_1500 / Paras.Yes	-0.02	-0.14	0.88
cranberry	shannonH_1500 / Paras.Yes	-0.03	-0.24	0.74
cranberry	ag_300 / ITfam	0.13	1.37	0.19
cranberry	open_300 / ITfam	-0.13	-1.36	0.18
cranberry	forest_edge_300 / ITfam	-0.05	-0.54	0.62

cranberry	shannonH_300 / ITfam	-0.12	-1.31	0.2
cranberry	ag_1500 / ITfam	0.14	1.45	0.15
cranberry	open_1500 / ITfam	0.01	0.02	0.99
cranberry	forest_edge_1500 / ITfam	0	-0.08	0.93
cranberry	shannonH_1500 / ITfam	0.11	1.18	0.27
cranberry	ag_300 / PDrar20	-0.05	-0.47	0.68
cranberry	open_300 / PDrar20	0.18	1.87	0.08
cranberry	forest_edge_300 / PDrar20	0.02	0.16	0.88
cranberry	shannonH_300 / PDrar20	0.09	0.87	0.42
cranberry	ag_1500 / PDrar20	-0.06	-0.66	0.55
cranberry	open_1500 / PDrar20	0.06	0.46	0.71
cranberry	forest_edge_1500 / PDrar20	0.03	0.27	0.82
cranberry	shannonH_1500 / PDrar20	-0.01	-0.08	0.95
cranberry	ag_300 / tongue	0.11	1.19	0.25
cranberry	open_300 / tongue	-0.15	-1.54	0.13
cranberry	forest_edge_300 / tongue	-0.01	-0.13	0.91
cranberry	shannonH_300 / tongue	-0.09	-0.9	0.39
cranberry	ag_1500 / tongue	0.07	0.72	0.5
cranberry	open_1500 / tongue	-0.06	-0.5	0.66
cranberry	forest_edge_1500 / tongue	-0.06	-0.64	0.58
cranberry	shannonH_1500 / tongue	0.06	0.6	0.6
blueberry	ag_300 / Nest_.cavity	-0.14	-0.76	0.52
blueberry	open_300 / Nest_.cavity	0.11	0.68	0.52
blueberry	forest_edge_300 / Nest_.cavity	0.1	0.61	0.64
blueberry	shannonH_300 / Nest_.cavity	0.09	0.53	0.69
blueberry	ag_1500 / Nest_.cavity	-0.34	-1.13	0.21
blueberry	open_1500 / Nest_.cavity	0.2	1.33	0.19
blueberry	forest_edge_1500 / Nest_.cavity	0.24	0.94	0.31
blueberry	shannonH_1500 / Nest_.cavity	-0.04	-0.25	0.82
blueberry	ag_300 / Nest_.hole	-0.03	-0.02	0.93
blueberry	open_300 / Nest_.hole	-0.02	-0.35	0.82
blueberry	forest_edge_300 / Nest_.hole	0.05	0.23	0.81
blueberry	shannonH_300 / Nest_.hole	0.07	0.4	0.72
blueberry	ag_1500 / Nest_.hole	0.08	0.52	0.44
blueberry	open_1500 / Nest_.hole	-0.05	-0.55	0.6
blueberry	forest_edge_1500 / Nest_.hole	0.01	0	1
blueberry	shannonH_1500 / Nest_.hole	0.05	0.29	0.71
blueberry	ag_300 / Nest_.soil	0.12	0.75	0.5
blueberry	open_300 / Nest_.soil	-0.12	-0.78	0.51
blueberry	forest_edge_300 / Nest_.soil	-0.05	-0.3	0.77
blueberry	shannonH_300 / Nest_.soil	-0.08	-0.47	0.67
blueberry	ag_1500 / Nest_.soil	0.41	1.28	0.14
blueberry	open_1500 / Nest_.soil	-0.09	-0.55	0.65
blueberry	forest_edge_1500 / Nest_.soil	-0.4	-1.48	0.08

blueberry	shannonH_1500 / Nest_.soil	-0.08	-0.48	0.72
blueberry	ag_300 / Nest_.wood	0.01	0.07	0.95
blueberry	open_300 / Nest_.wood	0.03	0.09	0.92
blueberry	forest_edge_300 / Nest_.wood	-0.07	-0.54	0.74
blueberry	shannonH_300 / Nest_.wood	-0.02	-0.19	0.92
blueberry	ag_1500 / Nest_.wood	-0.15	-0.48	0.52
blueberry	open_1500 / Nest_.wood	-0.12	-0.93	0.4
blueberry	forest_edge_1500 / Nest_.wood	0.25	1.07	0.18
blueberry	shannonH_1500 / Nest_.wood	0.15	0.85	0.33
blueberry	ag_300 / Socia.Eusocial	-0.17	-1.03	0.36
blueberry	open_300 / Socia.Eusocial	0.13	0.83	0.47
blueberry	forest_edge_300 / Socia.Eusocial	0.16	1.1	0.29
blueberry	shannonH_300 / Socia.Eusocial	0.13	0.84	0.42
blueberry	ag_1500 / Socia.Eusocial	-0.32	-1.04	0.38
blueberry	open_1500 / Socia.Eusocial	0.21	1.38	0.17
blueberry	forest_edge_1500 / Socia.Eusocial	0.2	0.77	0.67
blueberry	shannonH_1500 / Socia.Eusocial	-0.01	-0.02	0.98
blueberry	ag_300 / Socia.fac_social	0.08	0.7	0.5
blueberry	open_300 / Socia.fac_social	-0.06	-0.48	0.66
blueberry	forest_edge_300 / Socia.fac_social	-0.12	-1.09	0.29
blueberry	shannonH_300 / Socia.fac_social	-0.09	-0.76	0.46
blueberry	ag_1500 / Socia.fac_social	-0.12	-0.59	0.31
blueberry	open_1500 / Socia.fac_social	-0.18	-1.52	0.12
blueberry	forest_edge_1500 / Socia.fac_social	0.22	1.36	0.09
blueberry	shannonH_1500 / Socia.fac_social	0.13	1.19	0.26
blueberry	ag_300 / Socia.Solitary	0.11	0.67	0.55
blueberry	open_300 / Socia.Solitary	-0.08	-0.55	0.63
blueberry	forest_edge_300 / Socia.Solitary	-0.07	-0.44	0.67
blueberry	shannonH_300 / Socia.Solitary	-0.06	-0.38	0.74
blueberry	ag_1500 / Socia.Solitary	0.39	1.27	0.13
blueberry	open_1500 / Socia.Solitary	-0.08	-0.52	0.66
blueberry	forest_edge_1500 / Socia.Solitary	-0.34	-1.3	0.17
blueberry	shannonH_1500 / Socia.Solitary	-0.08	-0.51	0.73
blueberry	ag_300 / Paras.No	0	-0.71	1
blueberry	open_300 / Paras.No	0	0.65	1
blueberry	forest_edge_300 / Paras.No	0	-0.69	0.91
blueberry	shannonH_300 / Paras.No	0	0.43	0.88
blueberry	ag_1500 / Paras.No	0	0.69	0.99
blueberry	open_1500 / Paras.No	0	-0.7	0.97
blueberry	forest_edge_1500 / Paras.No	0	0.96	0.34

blueberry	shannonH_1500 / Paras.No	0	-0.72	0.88
blueberry	ag_300 / ITfam	-0.03	-0.13	0.9
blueberry	open_300 / ITfam	0.01	0.02	0.99
blueberry	forest_edge_300 / ITfam	-0.05	-0.33	0.78
blueberry	shannonH_300 / ITfam	-0.02	-0.16	0.88
blueberry	ag_1500 / ITfam	-0.42	-1.33	0.16
blueberry	open_1500 / ITfam	-0.02	-0.09	0.95
blueberry	forest_edge_1500 / ITfam	0.42	1.59	0.08
blueberry	shannonH_1500 / ITfam	0.12	0.73	0.52
blueberry	ag_300 / PDrar20	-0.08	-0.4	0.73
blueberry	open_300 / PDrar20	0.13	0.66	0.53
blueberry	forest_edge_300 / PDrar20	0	-0.02	0.98
blueberry	shannonH_300 / PDrar20	0.03	0.15	0.89
blueberry	ag_1500 / PDrar20	-0.42	-1.39	0.17
blueberry	open_1500 / PDrar20	-0.04	-0.19	0.87
blueberry	forest_edge_1500 / PDrar20	0.35	1.37	0.17
blueberry	shannonH_1500 / PDrar20	0.32	1.59	0.11
blueberry	ag_300 / tongue	-0.17	-0.91	0.41
blueberry	open_300 / tongue	0.05	0.29	0.82
blueberry	forest_edge_300 / tongue	0.08	0.41	0.72
blueberry	shannonH_300 / tongue	0.08	0.41	0.71
blueberry	ag_1500 / tongue	-0.48	-1.51	0.12
blueberry	open_1500 / tongue	0.07	0.35	0.73
blueberry	forest_edge_1500 / tongue	0.36	1.39	0.18
blueberry	shannonH_1500 / tongue	-0.02	-0.08	0.95

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684 Table S4: Model selection procedure showing all models within 2 AICc 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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