EDITOR'S CHOICE: REVIEW: Trait matching of flower visitors and crops predicts fruit set better than trait diversity

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Title: Trait matching of flower visitors and crops predicts fruit set better than trait diversity

Running title: *Trait matching and crop pollination*

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Summary

1. Understanding the relationships among trait diversity, species diversity, and ecosystem functioning is essential for sustainable management. For functions comprising two trophic levels, trait matching between interacting partners should also drive functioning. However, the predictive ability of trait diversity and matching is unclear for most functions, particularly for crop pollination, where interacting partners did not necessarily co-evolve.

2. Worldwide, we collected data on traits of flower visitors and crops, visitation rates to crop flowers per insect species, and fruit set in 469 fields of 33 crop systems. Through hierarchical mixed-effects models we tested whether flower-visitor trait diversity and/or trait matching between flower visitors and crops improve the prediction of crop fruit set (functioning) beyond flower-visitor species diversity and abundance.

3. Flower-visitor trait diversity was positively related to fruit set, but surprisingly did not explain more variation than flower-visitor species diversity.

4. The best prediction of fruit set was obtained by matching traits of flower visitors (body size and mouthpart length) and crops (nectar accessibility of flowers) in addition to flower-visitor abundance, species richness, and species evenness. Fruit set increased with species richness, and more so in assemblages with high evenness, indicating that additional species of flower visitors contribute more to crop pollination when species abundances are similar.

5. *Synthesis and applications*. Despite contrasting floral traits for crops worldwide, only the abundance of a few pollinator species is commonly managed for greater yield. Our results suggest that the identification and enhancement of pollinator species with traits matching those of the focal crop, as well as the enhancement of pollinator richness and evenness, will increase crop yield beyond current practices. Furthermore, we show that field practitioners can predict and manage agroecosystems for pollination services based on knowledge of just a few traits that are known for a wide range of flower-visitor species.

Introduction

Sustainable management of agroecosystems is a global challenge, with more than 35% of Earth's land area covered by farmland (FAO 2013). It has been suggested that species diversity is critical for sustainability because it increases the level and stability of agroecosystem functioning, represented by measures of ecosystem services and agricultural production (Cardinale *et al.* 2012; Bommarco, Kleijn & Potts 2013). There is a growing consensus that such influences of species diversity on functioning are mediated by changes in trait diversity (Díaz & Cabido 2001; Cadotte, Carscadden & Mirotchnick 2011; Cardinale *et al.* 2012; Fründ *et al.* 2013). However, empirical evidence for the role of trait diversity on agroecosystem functioning is scarce (Martins, Gonzalez & Lechowicz 2015).

Trait diversity reflects the among-species variation in morphological, physiological, and behavioural traits relevant to a specific function. Hence, newly developed indices of trait diversity are expected to better predict functioning than traditional indices of species diversity (Díaz & Cabido 2001; Cadotte, Carscadden & Mirotchnick 2011; Schleuning, Fründ & García 2015). To become a parsimonious and practical tool for predicting functioning, i.e. high goodness of fit and low complexity, trait diversity should be based on fewer traits than species. This occurs when some species share similar traits, known as partial functional redundancy (Cadotte, Carscadden & Mirotchnick 2011). Alternatively, if increased functioning is caused by numerous traits with low redundancy among species, trait and species diversity will perform similarly in explaining functioning. In such cases, species diversity will be a good proxy of trait diversity. To date, the few studies on the relationship between trait and species diversity have revealed mixed results (reviewed by Cadotte, Carscadden & Mirotchnick 2011; Schleuning, Fründ & García 2015). Furthermore, most of the evidence on the role of trait diversity is based on studies using primary production in plant communities as the targeted function (Díaz & Cabido 2001; Díaz *et al.* 2007), whereas this relationship remains unresolved for most functions driven by plant–animal interactions (Cadotte, Carscadden & Mirotchnick 2011; Gagic *et al.* 2015; Schleuning, Fründ & García 2015).

The relative abundance of a certain trait state in the community, hereafter trait identity, may predict functioning independently of trait or species diversity. Trait identity should be an important predictor when there is a trait state that performs best for a given function (Díaz *et al.* 2007; Mokany, Ash & Roxburgh 2008) and when functioning increases with the abundance of species carrying that trait state (mass ratio hypothesis) (Grime 1998). If so, abundant species should have greater influence on trait identity and consequently on functioning than their less common counterparts (Grime 1998; Díaz *et al.* 2007; Mokany, Ash & Roxburgh 2008).

For functions comprising two trophic levels, trait identity effects may depend on the matching of trait states between interacting partners, hereafter trait matching (Schleuning, Fründ & García 2015). For example, the effect of the abundance of herbivores on primary production depends on the match between grazing habit and plant life forms (Asner *et al.* 2004). Trait matching between individual species of plants and animals resulting from co-evolution has been examined in the scientific literature (e.g. Stang, Klinkhamer & van der Meijden 2006; Vázquez et al. 2009; Junker et al. 2013), but its effects on functioning at the community level have not (but see Fontaine et al. 2006), especially for crop pollination, where in many regions crops are exotic but pollinators are native, without a co-evolutionary history.

Our objective was to assess whether trait diversity and/or matching contributed to crop fruit set (functioning), above and beyond the predictive ability of flower-visitor species abundance and diversity. Fruit set, the proportion of a plant's flowers that develop into mature fruits or seeds, reflects pollination success when other resources (e.g. nutrients) are not limiting (Wesselingh 2007). Fruit set is a key component of agricultural yield, and has been shown to increase with the abundance and richness of wild insects visiting crop flowers (Garibaldi *et al.* 2013). Such dependency may be explained by pollinator trait diversity and/or matching. For example, social and solitary bees visited flowers on radishes at different times of day, suggesting temporal complementarity among these pollinator groups (Albrecht *et al.* 2012). Insects with distinctive mouthpart lengths, hoverflies vs. bumble bees, complemented each other in the pollination of flowers with easily accessible rewards vs. those with rewards hidden at the bottom of a tubular corolla, respectively (i.e. trait matching) (Fontaine *et al.* 2006; Campbell *et al.* 2012). Small sized bees transported less pollen to pumpkin flowers than bigger bees, but this pollen was distributed more uniformly on the stigma (Hoehn *et al.* 2008). Here, we collected data on traits of flower visitors and crops, visitation rates to crop flowers per insect species, and fruit set in 469 fields of 33 crop systems all over the world. This synthesis provides a unique opportunity to test the strength of the relationship between trait and species diversity, and of the relative ability of trait vs. species indices for predicting functioning, across contrasting crop systems. Our results show that trait matching between flower visitors and crops, but not trait diversity, improves our ability beyond species abundance and diversity, to predict and understand the spatial variation in crop fruit set.

Materials and methods

Field sampling

We collected data from crops on all continents (except Antarctica) matching the following selection criteria: (i) data sampled from at least four spatially separated fields; (ii) observations of insect species visiting crop flowers in the sampled fields; (iii) information on traits of flower visitors; (iv) an estimate of fruit or seed set as the percentage of flowers setting mature fruits or number of seeds per flower, respectively (hereafter fruit set) and (v) at least partial dependence on flower visitors for maximum fruit set. This led to a total of 33 crop systems distributed among 469 fields (see Appendix S1 in Supporting Information), with a crop system defined as a single crop species in a particular region in a single study. Eight of the 33 crop systems have not been included in a previous synthesis (Garibaldi *et al.* 2013), namely apple in the UK, black cardamom in India, cardamom in India, field bean in the UK, oilseed rape in Sweden, strawberry in Germany, strawberry in the UK, and strawberry in the USA (Appendix S2, Table S1). Furthermore, for all crop systems, data on traits are presented here for the first time. The sampled fields were subjected to a diversity of agricultural practices, including large monocultures and small and diverse cultivations. A wide array of annual and perennial fruit, seed, nut, and stimulant crops was included.

In each field, we measured flower visitation per unit of time and flower for each insect species, from which we estimated species richness and evenness. Bee taxa observed in many crop systems (Table S2) included apex-furrowed (or sweat) bees (Halictidae), bumble bees (Apidae: *Bombus* spp.), carpenter bees (Apidae: Xylocopini), plasterer bees (Colletidae), sand bees (Andrenidae), small carpenter bees (Apidae: Ceratinini), stingless bees (Apidae: Meliponini), the eastern honey bee *Apis cerana*, the giant honey bee *Apis dorsata*, and the western honey bee *Apis mellifera*. In some crop systems, ants (Hymenoptera: Formicidae), syrphid flies (Diptera: Syrphidae), other flies, and various beetle species (Coleoptera) were common flower visitors. We also measured fruit set, which is usually correlated with crop yield across fields (e.g. see Figure S1 in Garibaldi *et al.* 2013). Given that we measured fruit set in several plants open to insect pollination per field, our results properly represent field conditions and are not biased by resource translocation among different developing fruits within plants (Wesselingh 2007).

Trait diversity

If trait indices are to be employed by field practitioners for predicting and managing agroecosystem functioning, they should be based on relatively few and relevant traits, for which there is accessible information for a wide range of flower-visitor species. We measured eight traits of the flower visitors that were expected to influence pollinator efficiency and therefore fruit set (Fontaine *et al.* 2006; Hoehn *et al.* 2008; Albrecht *et al.* 2012; Martins, Gonzalez & Lechowicz 2015). Sociality (yes vs. no) was defined as colony building, including all eusocial as well as semi-social species (Table S2). Oligolectic (yes vs. no) included flower visitors that collect pollen from one or a few closely related plant species, whereas polylectic species collect pollen from a variety of flowers belonging to different plant families. Seasonal activity (complete vs. partial) (Junker *et al.* 2013) was classified according to whether the pollinator species visit the crop during the whole flowering period or only during early or late periods. Cleptoparasitic (yes vs. no) was defined as flower visitors that lay eggs in the nests of other insect species (e.g. cuckoo bees). Cleptoparasitic insects do not actively collect pollen, which may impair their efficiency as crop pollinators. Body size was defined according to the intertegular span (ITD), the distance between the two insertion points (tegula) of the wings of female workers of each species. Body size classes for bees were as following: tiny (< 1.5 mm ITD, typical foraging distance < 50 m), small (1.5–2.0 mm ITD, typical foraging distance 50–300 m), medium (2–3.3 mm ITD, typical foraging distance 300–1100 m), and large (> 3.3 mm ITD, typical foraging distance > 1100 m) (Greenleaf *et al.* 2007). We follow the same classification for syrphids for consistency and butterflies and moths were commonly classified as large. Mouthpart length, i.e. tongue or proboscis, was classified as short (< 3 mm), medium (3–8 mm) or long (> 8 mm; see figure 1 in (Stang, Klinkhamer & van der Meijden 2006). Finally, we classified flower visitors according to whether they are capable of buzz pollination (yes vs. no), and if they were central place foragers (yes vs. no). As our study represents a major effort of data sampling at a global scale, we could not measure intra-specific differences for all flower-visitor species in all crop systems and we focus only on inter-specific differences (i.e. mean values per species for all crop systems). However, except for size measurement (body and mouthparts), these traits (e.g. sociality) are not likely to vary among individuals within a species.

Crops were also classified according to four traits expected to be relevant for pollination success (Table S1) (Fontaine *et al.* 2006). Flower diameter at the widest part of the flower was classified as small (1–10 mm), medium (> 10–35 mm), or large (> 35 mm). Nectar accessibility, high vs. low, reflected the accessibility of the nectar resources (nectaries) to the flower visitors (Stang, Klinkhamer & van der Meijden 2006; Fontaine *et al.* 2006; Junker *et al.* 2013). Crops with low nectar accessibility had narrow or tubular flowers, and showed a ratio between flower diameter (mm) and the distance of the nectaries to the anthers (mm) lower than 1.5. Generally, crops with less accessible nectar are expected to suffer a greater degree of nectar robbery (e.g. see page 178 for oilseed rape in Free 1993). For acerola and annato, crops that do not secrete nectar, the classification refers to accessibility of oil and pollen, respectively. Pollinator dependence was defined as the percentage of yield reduction in the absence of pollinators (Klein *et al.* 2007). We also classified crops according to their typical duration of flowering into short (< 10 days per plant), medium (10–25 days), or long (> 25 days).

We chose three complementary, uncorrelated, trait diversity indices (Laliberté & Legendre 2010; Mouchet *et al.* 2010) and calculated these indices using the eight traits of flower visitors described above as predictors of fruit set. Trait richness, defined as the total branch length of a trait dendrogram, measures the extent of trait complementarity among species (Petchey & Gaston 2006). This index is highly correlated with the trait richness proposed by Villéger, Mason & Mouillot (2008) but allows quantification of assemblages with low species richness. Trait evenness is defined as the regularity of the abundance distribution in the volume of the trait space occupied by the pollinator assemblage (Villéger, Mason & Mouillot 2008). Trait dispersion is defined as the mean distance in multidimensional trait space of individual species to the centroid of all species, and is mathematically related to Rao's Q (Laliberté & Legendre 2010).

The community weighted mean (hereafter, CWM) is a single trait index that provides an estimate of the trait states that dominate in a community (i.e. trait identity; Díaz *et al.* 2007). It is calculated by weighting the measure of a trait by the relative abundance of all species carrying that trait, and summing over all trait states. For example, CWMs for body size range from zero when all species in a field are tiny to four when all species are large, whereas CWMs for sociality range from zero when all species are solitary to one when all species are social. Package FD (R Development Core Team 2013) and publicly-available code (https://github.com/ibartomeus/fundiv) were used to calculate all indices.

Statistical analyses

Observations for fruit set and each predicting variable (y) in each field (i) of each crop system (j) were standardized using z-scores ($z_{ij} = \frac{(y_{ij} - \bar{y}_j)}{SD_j}$) to allow comparisons among crop systems, despite contrasting means ($\bar{y}_j$) and standard deviations (SD_j), and differences in methodology. Unlike other standardizations, such as logarithms, z-scores do not modify the form (e.g. linear or curvilinear) of the relationship between response and predicting variables. Furthermore, z-scores allow for direct comparison of the values of the partial regression coefficients, and therefore are useful for understanding the relative effects of predicting variables.

We evaluated how trait richness varied with species richness across fields (and the same for trait and species evenness). In case of functional redundancy, trait richness would increase with species richness across sites with a regression coefficient < 1. Alternatively, in the case of little functional overlap between species, an approximately one to one relationship would be expected (see Introduction). Because both trait and species richness are random variables, model I regressions (e.g. through ordinary least squares) will underestimate the slope of the linear relationship (see section 10.3.2 of Legendre & Legendre 1998). Instead, we performed model II regressions, as the emphasis was not on forecasting trait richness but on estimating the correct value of the slope for the relationship between trait and species richness (R software version 3.0.2, lmodel2 package, lmodel2 function) (R Development Core Team 2013; Legendre 2014). Among the estimation methods for model II regressions, we chose major axes because both variables were in the same units (z-scores), variance of error was about the same for both variables, and distribution was approximately bivariate normal (Legendre & Legendre 1998).

To forecast fruit set, we estimated the influences of *a priori* selected combinations of predicting variables through general linear mixed-effects models (R software version 3.0.2, nlme package, lme function, with Gaussian error distribution) (R Development Core Team 2013;

Pinheiro *et al.* 2014), which are effective for integrated analysis of data from many sources (Qian *et al.* 2010). This approach produces similar results to Bayesian hierarchical models when uninformative priors are employed, especially with large samples, as in our case (Gelman & Hill 2007; Qian *et al.* 2010). By including crop system as a random variable, our models estimated intercepts (α_j) for each system (j) to account for the hierarchical data structure and differences among systems (random intercept models) (Gelman & Hill 2007; Qian *et al.* 2010). Each partial regression coefficient (β_+) was considered a fixed effect reflecting the influence of a predicting variable on fruit set over all crop systems. We tested the Gaussian and homoscedasticity assumptions for the standardized residuals of the models with graphical analyses and Kolmogorov-Smirnov tests (Type I error rate = 0.05). These assumptions were valid in all cases.

To test whether trait diversity better predicts fruit set than species diversity, we compared Akaike's Information Criterion (hereafter, AIC) values for three *a priori* models (Table S3). All models included visitation rate to control for abundance variation among fields, combined with either species richness and evenness based on Pielou's J (model A), trait richness and evenness (model B), or trait dispersion (model C) as predicting variables. Model B is conceptually equivalent to model A but used trait instead of species diversity indices, whereas model C was included to be comprehensive in the trait indices employed (see previous section). In the three models we estimated all possible interactions among predicting variables. We expected models B and C to show lower AIC than model A (see second paragraph of the Introduction). We also present a fourth "best" model, which was the one with the lowest AIC, after evaluating the models resulting from all possible combinations of the six predicting variables (visitation rate, species richness, species evenness, trait richness, trait evenness, and trait dispersion) and their paired interactions (MuMIn package, dredge function) (Bartoń 2014). The four models were compared to a fifth, "null" model without any fixed predicting variable to understand if they provide any relevant fit. The five models did not present multicollinearity, and all variance inflation factors (VIFs) were lower than 1.4 (see also Table S4). AIC values were obtained based on maximum likelihood estimates of regression coefficients, because models differed in the fixed structure but shared the same random structure (random intercepts for different crop systems), whereas parameter estimates for models presented in tables and figures were obtained using the restricted maximum likelihood method (Zuur *et al.* 2009).

It is important to note that evenness indices have different approaches for weighting rare and common species and this can influence the results (Ricotta & Avena 2003; Marini *et al.* 2014). Therefore, we repeated the analyses using nine other evenness indices, including Evar, inverse of Simpson index, and seven evenness profiles covering the entire spectrum of weights for dominant species (Ricotta & Avena 2003; Marini *et al.* 2014). These analyses did not modify our conclusions based on Pielou's *J* (data not shown).

Finally, we evaluated how individual traits of flower visitors and crops (trait identity and matching) might increase our ability to predict fruit set. Specifically, we compared AIC of four *a priori*, mixed-effects models of the influences of selected crop traits, CWM of flower visitor traits, and their interaction on fruit set (Table S5). An interaction between crop traits and flower visitor traits indicates trait matching, whereas no interaction indicates that a given trait is best for all crops (i.e. only trait identity). In addition, the models always included all the fixed effects of the best model tested in Table S3. Among the eight traits measured for flower visitors, we selected three for which we had *a priori* expectations (Stang, Klinkhamer & van der Meijden 2006; Fontaine *et al.* 2006; Hoehn *et al.* 2008; Albrecht *et al.* 2012; Martins, Gonzalez & Lechowicz 2015) and for which we found variation within and across studies, namely sociality, mouthpart length, and body size (e.g. little variation was found for cleptoparasitism, as most flower visitors were non-cleptoparasitic, see Results section). Similarly, we selected four relevant crop traits: nectar accessibility, degree of pollinator dependence, flower diameter, and flowering length. The four models included the three selected flower-visitor traits but varied in the crop trait considered to evaluate trait matching. We always estimated all possible interactions among predicting variables. We also compared these four *a priori* models with the previous best model, with the null model, and with the model with the lowest AIC after evaluating the models resulting from all possible combinations of the predicting variables and their pair interactions (MuMIn package, dredge function) (Bartoń 2014). None of the models presented multicollinearity, and all VIFs were lower than 2 (see also Table S4).

Results

Crop flower visitors were typically polylectic, non-cleptoparasitic, central place foragers, and active during the whole flowering period of the crop (Table S2). However, flower visitors had contrasting mouthpart lengths, body sizes, social behaviour, or buzz pollination behaviour. Community weighted means for these traits did not differ among crops with high vs. low nectar accessibility (Fig. S1), different flower diameter, pollinator dependence, or flowering length, as linear mixed-effects models including crop traits as predictors of CWMs showed no improvement (lower AIC) to null models. On average, fields with bigger flower visitors (CWMs for body size) also had greater dominance of flower visitors with larger mouthparts (CWMs for mouthpart length; Fig. S2, Table S4).

Trait and species richness were strongly and positively associated across fields, indicating low redundancy among species of flower visitors (Fig. 1). Similarly, trait and species evenness were positively associated across fields. In both cases, the slopes of the model II regressions did not differ from a one to one relationship (Fig. 1), as denoted by the 95 % confidence intervals (CI richness: 0.90–1.13; CI evenness: 0.85–1.34). We found no clear improvement (lower AIC) when considering curvilinear relationships between trait and species richness (or evenness), and therefore we present only models with linear form. In addition, there was no benefit of including crop system specific slopes or intercepts (Fig. S3).

Fruit set increased with trait and species diversity of flower visitors across fields worldwide (models A and C in Table S3). However, trait diversity did not improve model fit on fruit set beyond species diversity, as models including trait diversity indices did not achieve lower AIC (compare models B and C to model A). The model with the lowest AIC included visitation rate, species richness, species evenness using Pielou's J, and richness × evenness interaction (model "best"). Fruit set increased linearly with species richness of flower visitors, but richness effects were greater in fields with high species evenness as denoted by a positive richness × evenness interaction (Fig. 2). The relationships of fruit set with species richness and evenness were independent of visitation rate, which was also positively associated to fruit set and showed the highest partial regression coefficient. In our synthesis, richness ranged between 0 (zero visits recorded in those fields) and 28 species, with a mean value of 7 species per field (the median was 6 species per field). For evenness, we found all the possible range of values for Pielou's J (from 0 to 1) showing a mean of 0.67 per field (the median was 0.73 per field). For visitation rate and species richness, we tested models with both linear and curvilinear (i.e. second order polynomial) forms. We found no clear improvement (lower AIC) when considering curvilinear relationships in mixed-effects models, and therefore we present only models with linear form. In addition, inclusion of system-specific partial regression coefficients (β_j) for each of the predicting variables (random slopes) in the best model did not decrease AIC, showing that the fixed effects (β_+) considered explained the heterogeneity of responses among crop systems.

In contrast to trait diversity, models including information on trait identity and matching increased model fit beyond species diversity and visitation rate (see models in Table S5). Specifically, the model with the lowest AIC (model "best") included as predictors of fruit set the CWM of sociality, body size, and mouthpart length, the nectar accessibility of the flowers, and the interactions (trait matching) of CWM for body size and mouthpart length with the nectar accessibility, in addition to visitation rate, species richness, species evenness, and richness ×

evenness interaction. Fruit set of crops with less accessible nectar decreased at fields with flower visitors of larger bodies and shorter mouthparts (Fig. 3; Fig. S4), whereas crops with more accessible nectar showed the opposite pattern (Fig. 3; Fig. S5). The values (in z-score scale) of the partial regression coefficients (β_+) for the interactions (trait matching) of CWM for body size and mouthpart length with the nectar accessibility were the greatest (Table S5). The β_+ values for visitation rate, species richness, and species evenness were similar to the ones obtained from a previous model ("best" in Table S3) that did not include as predicting variables aspects of trait identity and matching, reflecting their independent contribution to model fit on fruit set. Similarly, our results were not confounded by differences in crop management system (Table S6). The effects of CWM for sociality on fruit set were not clear.

Discussion

If trait diversity indices predict functioning better than species diversity indices, it suggests that there are a subset of traits shared across species that are overwhelmingly important for functioning. Contrary to this idea, here we demonstrate that although trait diversity indices were positively related to crop fruit set (functioning), they did not provide greater model fit compared to species diversity indices (including both richness and evenness). Furthermore, we found very low functional redundancy among flower-visitor species, suggesting that there is not enough sharing of important traits among species to make the trait diversity indices more useful than species diversity.

Worldwide, we found positive and linear (one to one) relationships between trait and species richness across 33 crop systems. It is important to note that trait richness increases, and functional redundancy decreases, with the number of traits included in richness indices (Cadotte, Carscadden & Mirotchnick 2011). In our synthesis, the low functional redundancy across flower-visitor species was mainly related to different combinations of mouthpart lengths, body sizes, social behaviour, and buzz pollination behaviour. Therefore, our results cannot be explained by an excess of traits, but by the variation across species in the *a priori* selected morphological and behavioural traits known to affect pollination efficiency (Fontaine *et al.* 2006; Hoehn *et al.* 2008; Campbell *et al.* 2012; Albrecht *et al.* 2012; Martins, Gonzalez & Lechowicz 2015). In contrast, previous evidence indicated that the relationship between trait and species diversity was complex and context dependent (Cadotte, Carscadden & Mirotchnick 2011). This lack of consistency across studies may reflect different criteria for trait selection, a limitation that was overcome in our synthesis.

The failure of trait diversity indices to improve predictions of fruit set is not explained by a lack of information on key traits in our synthesis, because we did find important trait effects, as specific combinations of individual traits of flower visitors and crops (i.e. interactions) increased model fit to species diversity. Specifically, flower visitors with large bodies and short mouthparts were more effective on crops with high rather than low nectar accessibility (i.e. trait matching). These results agree with previous studies on wild plants that thoroughly discussed the benefits of longer pollinator mouthparts for narrow or tubular flowers (Fontaine *et al.* 2006; Campbell *et al.* 2012). However, here we could test the effects of body size and mouthpart length on functioning after accounting statistically for the co-variation between both, and our findings on body size are in contrast to previous studies that could not separate these effects (Fontaine *et al.* 2006; Campbell *et al.* 2012). Larger bodies may deposit more pollen (e.g. Hoehn *et al.* 2008) and can increase the probability that pollinators contact the reproductive parts of crops with open flowers and accessible nectar. Examples in our data include the larger bodies but similar mouthparts of *Xylocopa frontalis* and *X. grisescens* vs. *Apis mellifera* making the former more effective pollinators of passion fruit (Fig. S5, Table S2). Such benefit of increased body size for improved pollination may not be shared in crops with more compact flower structures and less accessible nectar. Reasons for this may be related to nectar robbery and flower damage (Morris, Vázquez & Chacoff 2010; Aizen *et al.* 2014), which are more likely by larger insects possessing stronger mandibles. For example, rates of raiding the relatively inaccessible nectar of field bean flowers can be higher for larger *Bombus terrestris* when compared to the smaller *Apis mellifera*, despite similar mouthpart lengths (Fig. S4, Table S2; for nectar robbery data see Garratt *et al.* (2014). These potential mechanisms should be tested in experimental studies.

Our results agree with studies on wild plants that emphasize the role of trait matching in structuring plant–pollinator networks (Stang, Klinkhamer & van der Meijden 2006; Vázquez *et al.* 2009; Junker *et al.* 2013). Here, we further demonstrate that trait matching increases functioning at the agroecosystem level across crops worldwide, independently of the positive contribution of species abundance, richness, or evenness. Moreover, in relative terms, the effects (partial regression coefficient values) of trait matching on functioning were even greater than the effects of species abundance, richness, or evenness.

The positive effect of species richness on fruit set was stronger in fields with high species evenness, suggesting that additional species contribute more to agricultural functioning when their abundances are more similar. Effects of species richness and evenness were independent from those of visitation rate (abundance), which agrees with other results suggesting that increasing pollinator diversity enhances pollination (e.g. Schleuning, Fründ & García 2015)). These effects are expected because of different non-exclusive mechanisms (Tscharntke *et al.* 2005), including pollination niche complementarity (Hoehn *et al.* 2008; Fründ *et al.* 2013), interspecific interactions such as synergism (Greenleaf & Kremen 2006; Carvalheiro *et al.* 2011; Brittain *et al.* 2013), or sampling effects (Cardinale *et al.* 2006; Schleuning, Fründ & García 2015). However, our study contrasts with previous evidence (Garibaldi *et al.* 2013) in finding an effect of richness that is statistically independent from visitation rate (abundance), which could be a consequence of the different set of studies included in our synthesis (see Materials and methods). Furthermore, here we show for the first time an ubiquitous and strong positive interaction between the effects of richness and evenness. Pollinator evenness may enhance fruit set via pollination complementarity among flower visitors, or diminish it if a dominant species is the most effective pollinator (Hillebrand, Bennett & Cadotte

2008). Our results clearly point to the former, positive effect of species evenness on functioning. Moreover, a positive interaction between richness and evenness may further suggests synergistic interactions among species of flower visitors, such as has been found between honey bees and wild insects in the few studies on this topic (Greenleaf & Kremen 2006; Carvalheiro *et al.* 2011; Brittain *et al.* 2013). Previous studies have shown that agricultural expansion and intensification reduces both species richness of pollinator assemblages and wild insect visitation (e.g. Garibaldi *et al.* 2011). In contrast, the effects of agricultural expansion and intensification on species evenness have been rarely accounted for (Marini *et al.* 2014), but may also drive ecosystem functioning (Bommarco *et al.* 2012).

Sustainable intensification of agroecosystems represents one of the greatest challenges for humanity (Bommarco, Kleijn & Potts 2013). To succeed in this challenge it is critical to quantify the relationships among trait diversity, species diversity, and agroecosystem functioning (Schleuning, Fründ & García 2015). Here we show that crop fruit set, an important component of agricultural yield, can be increased through both higher species richness (showing a linear increase, ranging from 0 to 28 species in our synthesis) and evenness (ranging from 0 to 1 in our synthesis) of flower visitors. Fruit set might be further enhanced by agricultural practices targeted to promote specific flower visitors with traits that match those of the focal crop. Indeed, trait matching showed the greatest influence on fruit set. Current management practices for greater pollination, however, focus mostly on enhancing flower-visitor abundance, often of a single species, namely *Apis mellifera*. Although greater abundance is an important contributor to pollination function, our results show that it cannot replace the additional benefits of species richness, species evenness, and trait matching between flower visitors and crops.

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Data accessibility

The data sets supporting this article have been uploaded as online Supporting Information.

References

Aizen, M.A., Morales, C.L., Vázquez, D.P., Garibaldi, L.A., Sáez, A. & Harder, L.D. (2014) When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. *New Phytologist*, **204**, 322–328.

Albrecht, M., Schmid, B., Hautier, Y. & Müller, C.B. (2012) Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4845–4852.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. & Harris, A.T. (2004) Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, **29**, 261–299.

Bartoń, K. (2014) MuMIn: Multi-model inference. R package version 1.10.0.

Bommarco, R., Kleijn, D. & Potts, S.G. (2013) Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, **28**, 230–238.

Bommarco, R., Lundin, O., Smith, H.G. & Rundlöf, M. (2012) Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 309–315.

Brittain, C., Williams, N., Kremen, C. & Klein, A.M. (2013) Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122767.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Campbell, A.J., Biesmeijer, J.C., Varma, V. & Wäckers, F.L. (2012) Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic and Applied Ecology*, **13**, 363–370.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D. a., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. & Jouseau, C. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, **443**, 989–992.

Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S. & Nicolson, S.W. (2011) Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, **14**, 251–259.

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20684–20689.

FAO. (2013) FAOSTAT, http://faostat.fao.org/site/377/default.aspx#ancor

Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. (2006) Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, **4**, e1.

Free, J.B. (1993) *Insect Pollination of Crops*, Second. Academic Press, London, UK.

Fründ, J., Dormann, C.F., Holzschuh, A. & Tscharntke, T. (2013) Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, **94**, 2042–2054.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W.W. & Bommarco, R. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20142620.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R. & Klein, A.M. (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, **14**, 1062–1072.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N. & Klein, A.M. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science (New York, N.Y.)*, **339**, 1608–1611.

Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C. & Potts, S.G. (2014) The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation*, **169**, 128–135.

Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge, UK.

Greenleaf, S.S. & Kremen, C. (2006) Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13890–13895.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.

Hillebrand, H., Bennett, D.M. & Cadotte, M.W. (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, **89**, 1510–1520.

Hoehn, P., Tscharntke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2283–2291.

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H. & Stang, M. (2013) Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks (ed T-L Ashman). *Functional Ecology*, **27**, 329–341.

Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.

Laliberté, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, **91**, 299–305.

Legendre, P. (2014) lmodel2: Model II Regression. R package version 1.7-2.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology,* 2nd ed. Elsevier, Amsterdam.

Marini, L., Öckinger, E., Bergman, K.O., Jauker, B., Krauss, J., Kuussaari, M., Pöyry, J., Smith, H.G., Steffan-Dewenter, I. & Bommarco, R. (2014) Contrasting effects of habitat area and connectivity on evenness of pollinator communities. *Ecography*, **37**, 544–551.

Martins, K.T., Gonzalez, A. & Lechowicz, M.J. (2015) Pollination services are mediated by bee functional diversity and landscape context. *Agriculture, Ecosystems & Environment*, **200**, 12–20.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Morris, W.F., Vázquez, D.P. & Chacoff, N.P. (2010) Benefit and cost curves for typical pollination mutualisms. *Ecology*, **91**, 1276–1285.

Mouchet, M.A., Villéger, S., Mason, N.W.H. & Mouillot, D. (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**, 867–876.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–58.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & Team, R.D.C. (2014) nlme: Linear and nonlinear mixed effects models. R package version 3.1-117.

Qian, S.S., Cuffney, T.F., Alameddine, I., McMahon, G. & Reckhow, K.H. (2010) On the application of multilevel modeling in environmental and ecological studies. *Ecology*, **91**, 355–361.

R Development Core Team. (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricotta, C. & Avena, G. (2003) On the relationship between Pielou's evenness and landscape dominance within the context of Hill's diversity profiles. *Ecological Indicators*, **2**, 361–365.

Schleuning, M., Fründ, J. & García, D. (2015) Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant-animal interactions. *Ecography*, **38**, 1–13.

Stang, M., Klinkhamer, P.G.L. & van der Meijden, E. (2006) Size constraints and flower abundance determine the number of interactions in a plant flower visitor web. *Oikos*, **112**, 111–121.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.

Vázquez, D.P., Blüthgen, N., Cagnolo, L. & Chacoff, N.P. (2009) Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany*, **103**, 1445–1457.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–301.

Wesselingh, R.A. (2007) Pollen limitation meets resource allocation: towards a comprehensive methodology. *New Phytologist*, **174**, 26–37.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*, First. Springer, New York, USA.

Figure legends

Fig. 1. Globally, trait and species richness (or evenness) of insect visitors to crop flowers are strongly linked. Left panel: trait richness of flower visitors increases with species richness at an indistinguishable rate (solid line) from a 1:1 relationship (broken line) indicating low functional redundancy among species. Right panel: trait evenness also increases with species evenness at an indistinguishable rate (solid line) from a 1:1 relationship (broken line). The solid line is the overall regression where each point is a field in a crop system. Data from individual crop systems were standardized by z-scores prior to analysis, permitting comparison of fields across crop systems.

Fig. 2. Fruit set increases with species richness of flower visitors at a higher rate in assemblages with high (blue: fields with evenness higher than the 3rd quartile) than low evenness (orange: fields with evenness lower than the 1st quartile). The solid line is the overall regression where each point is a field in a crop system. Data from individual crop systems were standardized by z-scores prior to analysis, permitting comparison of fields across crop systems.

Fig. 3. Flower visitors with large bodies and short mouthparts are more effective on crops with high (open flowers) rather than low (narrow, tubular flowers) nectar accessibility. Data show fruit set of crops with high (orange) and low (blue) nectar accessibility as a function of community weighted means (CWM) of flower visitors for body size (upper panel) and mouthpart length (lower panel). The solid line is the overall (fixed-effect) prediction from the best model (Table S5), where each point is a field in a crop system. Data from individual crop systems were standardized by z-scores prior to analysis, permitting comparison of fields across crop systems. Flowers of almond (left) and red clover (right) are shown as examples of crops with high or low nectar accessibility, respectively (colours indicate nectar location within the flowers).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data supporting our results.

Appendix S2. Methods for unpublished studies.

Table S1. Plant traits and other characteristics of the 33 crop systems analyzed.

Table S2. Examples of abundant flower visitors and trait classification.

Table S3. Akaike's Information Criterion (AIC) and partial regression coefficients for mixed-effects models of the influences on fruit set, including for flower visitors: visitation rate, species richness, species evenness, trait richness, trait evenness, and trait dispersion.

Table S4. Correlation coefficients between the quantitative variables measured in our study.

Table S5. Akaike's Information Criterion (AIC) and partial regression coefficients for mixed-effects models of the influences on fruit set, including for flower visitors: visitation rate, species richness, species evenness, community weighted mean (CWM) of sociality, CWM of body size, and

CWM of mouthpart length.

Table S6. The inclusion of crop management practices, such as policulture *vs*. monoculture, do not influence our results.

Fig. S1. Sociality, body size, and mouthpart length of flower visitors do not differ between crops with high vs. low nectar accessibility.

Fig. S2. Community weighted means (CWMs) of body size and mouthpart length are positively related across crop fields globally.

Fig. S3. For contrasting crops worldwide, trait richness of flower visitors increases with species richness at a 1:1 relationship indicating low functional redundancy among species.

Fig. S4. Fruit set of crops with less accessible nectar generally decrease at fields with bigger flower visitors.

Fig. S5. In contrast to crops with low nectar accessibility, fruit set of crops with high nectar accessibility generally increase at fields with bigger flower visitors.