~~Effect~~ Relationships between~~of~~ wild bees, ~~and~~ hoverflies ~~on~~ and pollination success in apple orchards with different landscape contexts

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Running title: Importance of wild pollinators in apple orchards

Abstract

1. Pollination is an important ecosystem service as many agricultural crops such as fruit trees are pollinated by insects. Agricultural intensification, however, ~~has resulted~~is one of the main drivers resulting in a serious decline of pollinator populations worldwide.

2. In this study pollinator communities were examined in twelve apple orchards surrounded by either homogeneous or heterogeneous landscape in Hungary. Pollinators (honey bees, wild bees, hoverflies) were surveyed in the flowering period of apple trees. Landscape heterogeneity was characterized in circles of 300, 500 and 1000 m radius around each orchard using Shannon’s diversity and Shannon’s evenness indices.

3. We found that pollination success of apple was ~~only~~ significantly related to the species richness of wild bees, regardless the dominance of honey bees.

4. Diversity ~~and evenness~~ of the surrounding landscape matrix had a marginal positive effect on the species richness of hoverflies at 300m, positive effect on the~~and~~ species richness of wild bees at 500m radius circle, while evenness of the surrounding landscape ~~and~~ enhanced the abundance of wild bees at ~~300m and~~ 500m radius circle ~~respectively, while~~. ~~f~~Flower resources in the groundcover within the orchards supported honey bees.

5. Therefore maintenance of semi-natural habitats within 500m around apple orchards ~~and permanent groundcover vegetation within the orchards are~~is highly recommended to enhance ~~both honey bees and~~ wild pollinator communities~~,~~ and apple production.

Keywords: ecosystem services; groundcover vegetation; honey bee; landscape heterogeneity; spatial scales

Introduction

Apple is one of the -most important insect~~-~~ pollinated crops in the European Union, accounting for 16% of the EU’s total economic gains attributed to insect (particularly bee) pollination (Leonhardt *et al*., 2013). Most apple varieties are cross-pollinated and insect pollination not only affects the quantity of apple production, but can also have marked impacts on the quality of the fruits, influencing size, shape and their market price (Garratt *et al*., 2014a). The most common insect pollinator of apple is the honey bee (*Apis mellifera*~~),~~); however, it is not the most efficient one. It sometimes robs nectar from the apple flower without pollinating it, and makes fewer contacts with the stigma of the apple flower, compared to certain solitary bees (Delaplane & Mayer, 2000). Moreover the dramatic decline of honey bees ~~through~~ in several European countries has increased attention to other pollinating insects (Greenleaf & Kremen, 2006; Iler *et al*., 2013). Species of some wild bee genera such as *Osmia*, *Andrena*~~,~~ and *Bombus* are known to visit flowers at lower temperatures and deposit higher pollen loads than honey bees (Bosch & Blas, 1994). Hoverflies (Syrphidae) have also been observed with pollen loads containing a high proportion of compatible fruit pollen ~~Further insects other than bees observed with pollen loads containing a high proportion of compatible fruit pollen are some hoverflies (Sirphidae)~~ (Kendall, 1973).

In the temperate zone, pollinator insects are under threat from a number of limiting factors, such as ~~on a decline caused by~~ climate change (Rader *et al*., 2013), human disturbance (Goulson *et al*., 2008), agricultural intensification (Kearns *et al*., 1998; Steffan-Dewenter *et al*., 2005; Fitzpatrick *et al*., 2006; Memmott *et al*., 2007), and landscape fragmentation (Aizen & Feisinger, 2003; Diekötter & Crist, 2013), which leads to less effective pollination and reduces agricultural production (Floyd, 1992; Garibaldi *et al*., 2011a, 2013). ~~The d~~Different species or functional species groups respond differently to environmental change, and their spatial and temporal complementarity can help to buffer pollination services to environmental changes (Kremen *et al.*, 2002; Brittain *et al.*, 2013). Maintaining ~~D~~diverse communities, however, requires appropriate~~, extensive~~ orchard management practices (Morandin & Winston, 2005; Gabriel *et al.*, 2010) and a heterogeneous landscape structure with ~~efficient~~ certain amount of semi-natural habitats in the surroundings to provide suitable foraging and nesting resources through the year (Kremen *et al.*, 2002; Steffan-Dewenter, 2002; Holzschuh *et al.*, 2012). The interaction between landscape structure and crop management variables often drives the diversity and/or the abundance of wild pollinator communities (Holzschuh *et al.*, 2007; Rundlöf *et al.*, 2008; Batáry *et al.*, 2011). On organic farms near natural habitats native bee communities could provide full pollination services even for a crop with heavy pollination requirements, without the intervention of managed honey bees (Kremen *et al.*, 2002). Organic farms isolated from semi-natural habitats or intensively managed farms with ~~e.g.~~ high pesticide input experience greatly reduced diversity and abundance of native pollinators, resulting in insufficient pollination services and an increased need for managed beehives establishment (Kremen *et al.*, 2002). On the one hand, semi-natural habitats provide potential nesting sites and overwintering habitats (Kells *et al.*, 2001; Kells & Goulson, 2003), nectar and pollen sources via flowering plants (Kraemer & Favi, 2005; Laubertie *et al.*, 2012), which are often available in insufficient amount within the managed agricultural areas. On the other hand, locally available food resources like naturally regenerated field margins, less intensive soil management and the presence of groundcover vegetation within the orchards provide higher species richness of flowering plants, which might result in higher pollinator richness and abundance (Van Buskirk & Willi, 2004; Kuussaari *et al.*, 2011; Ricou *et al.*, 2014) and may enhance fruit production (Brittain *et al.*, 2013).

Apple is the most important fruit tree in Hungary, as it provides 60 % of the total Hungarian fruit production, and ~~produces~~ currently amounts to 400-600 thousand tons annually on 35,000 hectares (Apáti, 2010). The country, and the Central-Eastern European region in general, harbour rich wild pollinator communities compared to the more intensively managed Western European countries (Batáry *et al*., 2010)~~,~~; however, the economic impact of the wild pollinator-groups in orchards is not well studied (but see Mallinger & Gratton, 2015). The decreasing trends in the species richness and abundance of pollinators call for urgent need to better understand the role of honey bees and wild pollinators in apple production, and to give evidence on the local and landscape scale effects on their communities. The aims of our study were to identify (1) which pollinators are present in apple orchards during the flowering period, (2) the effect of surrounding landscape context on the pollinator communities within the orchards, (3) the role of weed management and vegetation composition within the orchards, (4) the linkage between amount of pollinators and fruit production depending on the landscape context or local scale effects.

Material and methods

Study area

Research was conducted in twelve commercial apple orchards in county Szabolcs-Szatmár-Bereg, Hungary, 2012. The orchards were at least 5 km apart, planted in 2002 and had the same variety of apple trees (*Malus domestica*, Relinda cultivar) with similar management on 3-7 hectares. The landscape structure in 1000 m radius around 6 orchards was homogeneous (>50% of arable field) and around 6 orchards heterogeneous (<30% of arable field). The landscape parameters within 1000, 500 and 300 m radius around the orchards were analyzed by CORINE Landcover maps (2006) and air photographs. We used different land-use categories to characterize the landscape structure such as orchard, forest, grassland, wetland, urbanised area and arable field. Landscape composition was characterized by the Shannon's Diversity Index (SHDI = -Σ (P * lnP), where *P* means the proportion of the buffer occupied by each land-use class defined before, and Shannon's Evenness Index (SHEI = SHDI / ln(m), where *m* is the number of land-use classes present in the landscape (Shannon & Weaver, 1949).

Regarding management practices, insecticide (2-5 times/year) and fungicide (6-7 times/year) ~~applications~~ were ~~made~~ applied in every orchard, mostly after the flowering period of apple, but in some orchards insecticide was used even before (in 7 orchards from the 12). In the tree rows herbicides (0-2 times/year) were used, alternatively the vegetation was mown or disc harrowed. In some orchards rotary tiller was used directly below the trees. The alleys between the tree rows ~~either~~ were either left unmanaged ~~for natural vegetation grow~~ or were managed with mechanical weed control ~~was used~~(see also Appendix 1).

Inventory methods for pollinators

Pollinators (honey bees, wild bees, hoverflies) were sampled during the flowering period of the apple trees (26 April – 1 May 2012). Every orchard was visited two times on two different days, once in the morning (9-12 a.m.) and once in the afternoon (2-5 p.m.) to avoid the heat at midday (>30 °C), when most insects are inactive. At each visit eight trees per orchard (altogether 192 trees) were observed for 15 minutes in a 2×2 m "window" of the canopy. The well-recognizable pollinators (honey bees, some bumblebee species) were recorded on the field, others were counted and (if possible) captured by insect net for later determination in the laboratory. The collected insects were determined at species level by specialists. Since honey bee individuals were visiting several flowers in a row, and usually foraged for a long time on the same tree~~were present usually during minutes on the same tree~~, they were counted only ~~in~~ every ~~fifth~~ five minutes during the observation period.

We assessed the number of apple blossoms in the observation window. The percentage of flowering plants in the undergrowth vegetation was assessed by visual observation in a 1 m radius circle below the centre of the canopy of the examined trees.

Measure of fruit production

We marked two branches of eight trees per orchard and approximately 30 flowers per branch were counted to calculate the fruit set. The number of developing green fruits was counted shortly after the end of flowering (June)~~ and the number of fruits during harvest as well~~.

Statistical analysis

We used the following response variables in our analysis: (i) *species richness* of hoverflies and wild bees (absolute richness according to the field data), (ii) *abundance* of honey bees and wild bees in apple orchards, and (iii) *pollination success* estimated as the number of green apples divided by the number of flowers at each selected branch.

Predictor variables acting at different spatial scales were applied as follows. At the level of trees, (square root transformed) number of apple flowers ~~on~~ and flower cover (%) in the undergrowth beneath the observed apple trees were used. At the level of orchards, the presence of insecticide treatment and presence of mechanical soil management (both in 2012 before the flowering period, see Appendix 1) were used, as well as the Shannon diversity index (SHDI) and Shannon evenness index (SHEI) characterizing landscape composition in circles of 300, 500 and 1000 m radius around each orchard.

We constructed generalized linear mixed models (GLMM) for each response variable. Species richness was analysed at the level of orchards, because the number of captured and identified wild bees and hoverflies was low at the level of individual apple trees, so here simple GLM was used without random effects. Consequently, here we only used predictors measured at the level of orchards. Pollinator abundance was analysed at tree level with orchard ID as a random factor. Data from the two sampling rounds (morning and afternoon observation) were treated separately during the analyses. Pollination success was analysed at branch level with hierarchical random factors (tree/orchard). Here species richness of hoverflies and wild bees and abundance of hoverflies, wild bees and honey bees were used as predictor variables. In models for the abundance and species richness a Poisson, and in the case of pollination success a normal error distribution was used, respectively.

We followed an automatic model selection procedure based on AICc values (Burnham & Anderson, 2002). First a full model was built for each response variable containing all predictors to be tested. If models contained landscape composition variables (abundance models), then a separate full model was constructed for each spatial scale to avoid using too many predictors and minimize multicollinearity. The list of full models can be found in Appendix 2. Then models with all possible combinations of predictors were fitted to the data and their AICc values were calculated. Parameter estimation and significance testing were done by averaging all models that had an AICc value not higher than the lowest AICc plus two ($\Delta AIC < 2$). In case of abundance models, where we had three full models according to the spatial scales, we accepted the estimation at only that scale where AICc values were the lowest, even if landscape variables were significant at other scales as well. We present the standard deviation of random effects and residuals of the best models (Appendix 3).

We also conducted a redundancy analysis (RDA) on species composition of wild bees (solitary bees + bumblebees) and all pollinators (wild bees + hoverflies). Constraint variables were insecticide use, SHDI and SHEI at 500 m, because these variables (except insecticide use) proved to have significant effects in the GLMMs. Significance of each variable was tested by permutation tests. Statistical analysis was conducted using packages 'lme4' (Bates *et al*., 2014), 'MuMIn' (Barton, 2014) and 'vegan' (Oksanen *et al*., 2013) of the R 3.1.2 statistical software (R Core Team, 2014).

Results

Altogether we observed 1574 individuals of 28 bee species (1442 individuals of honey bees and 132 individuals of wild bees including 104 and 28 individuals of solitary bees and bumblebees, respectively). 30 individuals of 13 hoverfly species were caught and altogether 66 individuals were observed (Appendix 4).

Species richness of pollinators showed a high variance among orchards (Appendix 1). We found no significant effects of any predictors on hoverfly species richness, it was only marginally significant related to SHDI at 300 m. Species richness of wild bees was significantly positively affected by SHDI at 500 m (Table 1).

Pollinators' abundance was dominated by honey bees. *Honey bee abundance* was significantly positively affected by the number of flowers on apple trees and percentage of flowering plants in the undergrowth, but no landscape scale effect was detected (Table 1, Fig. 1). *Abundance of wild bees* was significantly positively affected by SHEI at 500 m (Table 1, Fig. 2).

Pollination success was significantly positively influenced by the number of wild bee species, but no other significant effects were revealed (Table 1, Fig. 3). Appendix 3 represents the estimations for all models after model averaging.

Constraint variables in the RDA altogether explained 25.5% and 29.4% of total variance in species composition of wild bees and all pollinators, respectively. However, none of the constraint eigenvalues proved to be significant by the permutation tests.

Discussion

The importance of pollinators in orchards is well-known, but composition of pollinator communities and their effectiveness on apple pollination have only recently been studied (Garcia & Miñarro, 2014; Garratt *et al*., 2014b). According to our results, the dominant pollinator in apple orchards was the honey bee, probably due to the numerous beehives established by beekeepers around the orchards. In apple-dominated landscapes the abundance of honey bee can be two to four times higher than in landscapes dominated by grasslands and forests (Marini *et al*., 2012). In our study, the abundance of honey bees was associated with an increased ~~by the~~ number of apple flowers, but also by flowers in the groundcover vegetation below the trees. It means that ground management within the tree rows has an important ~~direct effect~~influence on the number of honey bees, through the number of flowers in the undergrowth. Native flowers within managed cultivars are beneficial for insect pollinators through diversity of food resources that is important for flower visitor health (Alaux *et al*., 2010), they improve stability of pollinator assemblages (Ebeling *et al*., 2008), and can even ~~ameliorate~~ mitigate negative effects of habitat management and/or habitat isolation from natural habitats (Carvalheiro *et al*., 2012). ~~A f~~Former ~~study~~ studies suggested reduced fruit set because of pollen competition with co-flowering plants (Schüepp *et al*.,

2013) and the removal of the ground vegetation to avoid potential competition with fruit trees for pollinators (Somerville, 1999).~~,~~ ~~h~~However, it was ~~debated~~ contradicted by other studies, which emphasised the strong positive effects of additional flower resources on bee abundances within cherry orchard (Holzschuh *et al.*, 2012). ~~As on the one hand t~~The presence of honey bees is strongly connected to the position of beehives, but ~~and on the other hand~~ honey bees fly even 3-4 kilometres from the hive to reach mass-flowering foraging patches if possible (Brittain *et al.*, 2013).~~,~~ ~~u~~Unsurprisingly, we found that honey bee ~~their~~ abundance was independent from the landscape context up to 1000m.

In contrast to honey bees, we found no direct link between undergrowth flower resources and wild bee abundance, which could be also the result of the only single sampling event during the year, missing the observation of potential long-term beneficiaries of ground cover on wild bees. Abundance of solitary wild bees is usually more influenced by local effects due to their smaller foraging range. Nevertheless, according to former studies maintaining living ground cover within commercial orchards could provide habitat and resources for potential wild pollinators, particularly native bees (Saunders *et al.*, 2013), and could provide benefits for apple growers by improving pollination services (Garcia, 2014).

~~In contrast, w~~Wild pollinators were influenced significantly by the surrounding landscape structure. The species richness of hoverflies was marginally significant related to landscape structure in 300 m, while species richness of wild bees was enhanced by landscape diversity within 500 m radius circle. Wild bee abundance showed a positive change in 500 m by Shannon's evenness index. Several former studies showed negative or positive effects of habitat quantity and quality of the surroundings (Banaszak, 1992; Kleijn & Langevelde, 2006; Kennedy *et al.*, 2013; Shackelford *et al.*, 2013; but see Steffan-Dewenter *et al.*, 2002; Westphal *et al.*, 2003). The impact of landscape structure varies between pollinator groups according to their mobility and foraging behaviour (Steffan-Dewenter *et al*., 2002; Steckel *et al*., 2014). ~~Abundance of solitary wild bees is usually more influenced by local effects due to their smaller foraging range.~~ Gathmann and Tscharntke (2002) found ~~that the~~a maximum foraging range ~~in the case~~ of solitary bees ~~is determined between~~of 150 and 600 m, while according to Jauker et al. (2013) 250 m radius around the center of the calcareous grasslands was the best scale predicting bee species richness.~~,~~ ~~t~~Therefore the amount of flowers and suitable nesting places within the orchard and/or in the adjacent environment has a great influence on solitary bee species richness and abundance. ~~Contrary~~ In contrast, Holzschuh et al. (2012) found ~~increased~~ wild bee visitation of cherry to increase with the proportion of high-diversity bee habitats in the surrounding landscape in 1 km radius. Although hoverflies can fly long distances and they do not have fix locations, their number is limited by resources of pollen and nectar and the availability of food for larvae (e.g. aphids).~~,~~ ~~t~~Therefore higher landscape diversity and evenness in the adjacent environment might enhance their number (Macleod, 1999; Ricou *et al*., 2014). Different land-use types provide sufficient habitat for feeding, laying eggs and larval development (Röder, 1990; Schweiger *et al*., 2007; Rotheray & Gilbert, 2011). Larvae of many hoverflies feed on aphids (Miñarro *et al*., 2005; Meyer *et al*., 2008) and a heterogeneous landscape with grasslands, orchards, but also arable fields may provide more food resource.

~~In contrast to honeybees, we found no direct link between undergrowth flower resources and wild bee abundance. Nevertheless, according to former studies maintaining living ground cover within commercial orchards could provide habitat and resources for potential wild pollinators, particularly native bees (Saunders *et al*., 2013), and could provide benefits for apple growers by improving pollination services (Garcia, 2014).~~

Although honey bees were observed in the highest abundance in the orchards, pollination success was influenced positively by the species richness of wild bees, even despite their low species number. Most ~~of the~~ solitary bees appear later in the year and in the case of bumblebees only queens are present in May (Michener, 2007). Positive effect of wild bees on crop pollination (e.g. apple, almond, cherry) has been already found in former studies (Williams & Thomson, 2003; Sheffield *et al.*, 2008; Garibaldi *et al.*, 2011b; Holzschuh *et al.*, 2012; Klein *et al*. 2012; Garratt *et al.*, 2014c). Similarly to our results, Holzschuh et al. (2012) found that although two thirds of all flower visitors were honey bees in cherry orchards, fruit set was related to wild bee visitation only, presumably due to their higher pollination efficiency. Our results correspond also with findings by Mallinger and Gratton (2015), who found similarly significant positive effect of wild bee species richness and no effect of honey bee abundance on apple fruit set. Several wild bee species show greater efficiencies and start foraging at lower temperatures than do honey bees (Torchio, 1991). For example *Osmia* species fly longer distances and change rows more frequently than honey bees, of which pollination efficiency seems to be limited mostly by the frequency of contact with the stigma of the flower (Bosch & Blas, 1994). According to former studies on sunflower and almond, increased pollination success by wild bee species richness might be also the result of enhanced honey bee pollination efficiency by interaction with wild bees (Greenleaf & Kremen, 2006; Brittain *et al.*, 2013). In our study there was no relationship between hoverflies ~~had no effect on~~and pollination success, which could be explained by their low abundance that might be the result of the single sampling event. However, some other studies found adults might be successful pollinators of other crops (McGuire & Armbruster, 1991; Larson *et al.*, 2001; Jauker & Wolters, 2008).

Conclusion

Honey bee is usually the most dominant and considered as the most important species in pollinator communities. However, wild bees or other wild pollinators can be more effective in apple pollination~~,~~ regarding their often higher frequency of contact with the stigma of the flower ~~that~~ compared to honey bees (Bosch & Blas 1994) ~~are unsuccessful in the pollination of some sorts of apple varieties, because they visit the flowers without contacting the stigmas~~. This study demonstrated the importance of both surrounding landscape diversity in 300-500m radius circle and flower resources in the groundcover within the orchards to enhance pollinator communities. Although we found no direct link between apple pollination success and landscape composition, the positive effects of landscape diversity on wild bees in the surroundings around the orchards support the former evidence that low habitat diversity can translate via reduced wild bee ~~visitation~~ species richness into a decline ~~in~~ of fruit set of an insect-pollinated crop (Holzschuh *et al.*, 2012). Therefore maintenance of semi-natural habitats within 500 m around orchards ~~and permanent groundcover vegetation within the orchards are~~is strongly advised to enhance ~~both honey bees and~~ wild pollinator communities~~,~~ and apple production.

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References

Aizen, M.A. & Feinsinger, P. (2003) Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation, in: Bradshaw, G.A., Marquet, P.A. (Eds.), How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas. Springer, Berlin, pp. 111−129.

Alaux, C., Ducloz, F., Crauser, D. & Le Conte, Y. (2010) Diet effects on honeybee immunocompetence. *Biology Letters*, **6**, 562–565.

Apáti, F. (2010) Az almaágazat helyzete és kilátásai az üzemgazdasági adatok tükrében. [The aspect of apple industry and outlooks in the light of the industrial data]. *Agrofórum Extra*, **33**, 44−46.

Banaszak, J. (1992) Strategy for conservation of wild bees in an agricultural landscape. *Agriculture, Ecosystems & Environment*, **40**, 179−192.

Barton, K. (2014) MuMIn: Multi-model inference. R package version 1.10.5. http://CRAN.R-project.org/package=MuMIn.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B*, **278**, 1894–1902.

Batáry, P., Báldi, A., Sárospataki, M., Kohler, F., Verhulst, J., Knop, E., Herzog, F. & Kleijn, D. (2010) Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agriculture, Ecosystems & Environment*, **136**, 35–39.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4_. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.

Bosch, J. & Blas, M. (1994) Foraging behaviour and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). *Applied Entomology and Zoology*, **29**, 1–9.

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,* **280**, 20122767.

Burnham, K.P. & Anderson, D.R. (2002) Model selection and multimodel inference. Springer, New York.

Carvalheiro, L.G., Seymour, C.L., Nicolson, S.W. & Veldtman, R. (2012) Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. *Journal of Applied Ecology*, **49**, 1373–1383.

Delaplane, K.S. & Mayer, N.F. (2000) Crop Pollination by Bees. CABI Publishing, Wallingford.

Diekötter, T. & Crist, T.O. (2013) Quantifying habitat-specific contributions to insect diversity in agricultural mosaic landscapes. *Insect Conservation and Diversity*, **6**, 607−618.

Ebeling, A., Klein, A., Schumacher, J., Weisser, W. & Tscharntke, T. (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, **117**, 1808-1815.

Fitzpatrick, Ú., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. & Brown, M.J.F. (2006) Rarity and decline in bumblebees-a test of causes and correlates in the Irish fauna. *Biological Conservation*, **136**, 185−194.

Floyd, W.D. (1992) Political aspects of set−aside as a policy instrument in the European Community, in: Clarke, J. (Ed.), Set-aside. The British Crop Protection Council. Monographs Series No. 50. The Lavenham Press Limited, Lavenham, pp. 13−20.

García, R.R. & Miñarro, M. (2014) Role of floral resources in the conservation of pollinator communities in cider-apple orchards. *Agriculture, Ecosystems & Environment,* **183**, 118−126.

Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A. & Harder, L.D. (2011a) Global growth and stability of agricultural yield decrease with pollinator dependence. *PNAS USA*, **108**, 5909−5914.

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. (2011b) 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.M., 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,* **339**, 1608−1611.

Garratt, M.P.D., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C. & Potts, S.G. (2014a) Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agriculture, Ecosystems & Environment*, **184**, 34−40.

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

Garratt, M.P.D., Truslove, C.L., Coston, D.J., Evans, R.L., Moss, E.D., Dodson, C., Jenner, N., Biesmeijer, J.C. & Potts, S.G. (2014b) Pollination Deficits In UK Apple Orchards. *Journal of Pollination Ecology*, **12**, 9−14.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**, 757−764.

Goulson, D., Lye, G.C. & Darvill, B. (2008) Decline and conservation of bumble bees. *Annual Review of Entomology*, **53**, 191−208.

Greenleaf, S.S. & Kremen, C. (2006) Wild bees enhance honey bees' pollination of hybrid sunflower. *PNAS*, **103**, 13890–13895.

Holzschuh, A., Dudenhöffer, J.-H. & Tscharntke, T. (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, **153**, 101–107.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, T. (2007) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.

Iler, A.M., Inouye, D.W., Høye, T.T., Miller-Rushing, A.J., Burkle, L.A. & Johnston, E.B. (2013) Maintenance of temporal synchrony between syrphid flies and floral resources despite differential phenological responses to climate. *Global Change Biology*, **19**, 2348−2359.

Jauker, F. & Wolters, V. (2008) Hover flies are efficient pollinators of oilseed rape. *Oecologia*, **156**, 819−823.

Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I. (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landscape Ecology*, **28**, 107−120.

Kearns, C.A., Inouye, D.W. & Waser, N.M. (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83−112.

Kells, A.R. & Goulson, D. (2003) Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems. *Biological Conservation*, **109**, 164−174.

Kells A.R., Holland J.M. & Goulson D. (2001) The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation*, **5**, 283−291.

Kendall, D.A. (1973) The viability and compatibility of pollen on insects visiting apple blossom. *Journal of Applied Ecology*, **10**, 847–853.

Kendall, D.A. & Smith, B.D. (1975) The foraging behavior of honeybees on ornamental *Malus* ssp. used as pollinizers in apple orchards. *Journal of Applied Ecology*, **12**, 465–471.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhoffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S. & Kremen, C. (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, **16**, 584−599.

Kleijn, D. & van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, **7**, 201−214.

Klein, A.M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N. & Kremen, C. (2012) Wild pollination services to California almond rely on semi-natural habitat. *Journal of Applied Ecology*, **49**, 723–732.

Kraemer, M.E. & Favi, F.D. (2005) Flower phenology and pollen choice of *Osmia lignaria* (Hymenoptera: Megachilidae) in Central Virginia. *Environmental Entomology*, **34**, 1593−1605.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *PNAS*, **99**, 16812–16816.

Kuussaari, M. Hyvönen, T. & Härmä, O. (2011) Pollinator insects benefit from rotational fallows. *Agriculture, Ecosystems & Environment*, **143**, 28–36.

Larson, B.M.H, Kevan, P.G & Inouye, D.W. (2001) Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Canadian Entomology*, **133**, 439–465.

Laubertie, E.A., Wratten, S.D. & Hemptinne, J.L. (2012) The contribution of potential beneficial insectary plant species to adult hoverfly (Diptera: Syrphidae) fitness. *Biological Control*, **61**, 1−6.

Leonhardt, S.D., Gallai, N., Garibaldi, L.A., Kuhlmann, M. & Klein, A.M. (2013) Economic gain, stability of pollination and bee diversity decrease from southern to northern Europe. *Basic and Applied Ecology*, **14**, 461–471.

MacLeod, A. (1999) Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) at an arable field margin with rich and poor floral resources. *Agriculture, Ecosystems & Environment*, **73**, 237−244.

Mallinger, R.E. & Gratton, C. (2015) Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology*, **52**; 323–330.

McGuire, A.D. & Armbruster, W.S. (1991) An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). *American Journal of Botany*, **78**, 214–219.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710−717.

Meyer, B., Jauker, F. & Dewenter, I.S. (2008) Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology*, **10**, 178–186.

Michener, C.D. (2007) The bees of the world, second ed. Johns Hopkins University Press, Baltimore.

Miñarro, M., Hemptinne, J.L. & Dapena, E. (2005) Colonization of apple orchards by predators of *Dysaphis plantaginea*: sequential arrival, response to prey abundance and consequences for biological control. *Biological Control*, **50**, 403−414.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B, Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.0-9. http://CRAN.R-project.org/package=vegan

R Development Core Team, R (2014) A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rader, R., James R., Bartomeus, I. & Winfree, R. (2013) Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, **19**, 3103−3110.

Ricou, C., Schneller, C., Amiaud, B., Plantureux, S. & Bockstaller, C. (2014) A vegetation-based indicator to assess the pollination value of field margin flora. *Ecological Indicators*, **45**, 320−331.

Rotheray, G.E. & Gilbert, F. (2011) The Natural History of Hoverflies. Forrest Text, Ceredigion, UK.

Röder, G. (1990) Biologie der Schwebfliegen Deutschlands (Diptera: Syrphidae) [Biologie of Germany's hoverflies (Diptera: Syrphidae)] Erna Bauer Verlag, Keltern−Weiler.

Rundlöf, M., Nilsson, H. & Smith, H.G. (2008) Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, **141**, 417–426.

Saunders, M.E., Luck, G.W. & Mayfield, M.M. (2013) Almond orchards with living ground cover host more wild insect pollinators. *Journal of Insect Conservation*, **17**, 1011–1025.

Schüepp, C., Herzog, F. & Entling, M.H. (2013) Disentangling multiple drivers of pollination in a landscape-scale experiment. *Proceedings of the Royal Society B*, **281**, 20132667.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekötter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J.P., Speelmans, M. & Dziock, F. (2007) Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*, **116**, 461−472.

Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C. & Sait, S.M. (2013) Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, **88**, 1002−1021.

Shannon, C.E. & Weaver, W. (1949) Mathematical Theory of Communication. University of Illinois Press.

Sheffield, C.S., Westby, S.M., Smith, R.F. & Kevan, P.G. (2008) Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. *The Canadian Entomologist*, **140**, 589−599.

Somerville, D. (1999) Honey bees in cherry and plum pollination, *NSW Agriculture Agnote* DAI 126.

Steckel, J., Westphal, C., Peters, M.K., Bellach, M., Rothenwoehrer, C., Erasmi, S., Scherber, C., Tscharntke, T. & Steffan-Dewenter, I. (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation*, **172**, 56–64.

Steffan-Dewenter, I., Münzenberg, U., Buerger, C., Thies,C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83**, 1421−1432.

Steffan-Dewenter, I., Potts, S.G. & Packer, L. (2005) Pollinator diversity and crop pollination services are at risk. *Trends in Ecology and Evolution*, **20**, 651−652.

Torchio, P.F. (1991) Bees as crop pollinators and the role of solitary species in changing environments. *Acta Horticulturae*, **288**, 49–61.

Van Buskirk, J. & Willi, Y. (2004) Enhancement of farmland biodiversity within setaside land. *Conservation Biology*, **18**, 987−994.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, **6**, 961−965.

Williams, N.M. & Thomson, J.D. (2003) Comparing pollinator quality of honey bees (Hymemoptera: Apidae) and native bees using pollen removal and deposition measures, in: Stickler, K., Cane, J.H. (Eds.), For nonnative crops, whence pollinators of the future? Entomological Society of America Lanham, Maryland, USA.

Table 1 Parameter estimates and AICc values of best models for each response variable. Significant predictors are bold. AICc weight indicates the probability that a given model is the best from a set of candidate models (models with ΔAICc < 2).

Response variable		Predictors	Estimate	*p*-value	AICc	AICc weight	Random effect SD	Residual SD
Species richness	Hoverfly	SHDI300	1.175 (± 0.662)	0.076	48.6	0.55		
	Wild bee	**SHDI500**	1.000 (± 0.368)	0.007	76.6	~1		
Abundance	Honeybee	**apple flower (sqrt)**	0.069 (± 0.006)	<< 0.001	1153.4	0.39	0.347	1.576
		undergrowth flower	0.012 (± 0.002)	<< 0.001				
		SHDI500	-0.524 (± 0.324)	0.105				
	Wild bee	**SHEI500**	6.480 (± 2.614)	0.013	420.8	0.19	0.751	1.053
		apple flower (sqrt)	0.032 (± 0.020)	0.101				
Pollination success		**Wild bee species richness**	0.009 (± 0.004)	0.044	-177.2	0.51	0.052	0.073

Figure legends

Fig. 1. Effects of flower number on and flower cover in the undergrowth beneath apple trees on honeybee abundance.

Fig. 2. Effect of SHEI at 500 m on the abundance of wild bees.

Fig. 3. Effect of wild bee species richness on pollination success.