

Effects of habitat fragmentation and disturbance on biodiversity and ecosystem functions

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General Introduction

Drivers and consequences of biodiversity change

Human growth in population and wealth leads to increasing demands of resources (Godfray et al. 2010). As a consequence, humans change ecosystems worldwide by modifying landscapes and climate, harvesting species, introducing invasive species, and the interaction of these factors, among others (Vitousek et al. 1997, Benayas et al. 2009, Ehrlich et al. 2012). These alterations undermine the environmental requirements of species and are considered as main drivers of biodiversity change (Sala et al. 2000). However, biodiversity is not only a product of the environment but also shapes biotic and abiotic conditions of an ecosystem by ecosystem functions (Lawton 1994). Therefore, changes of biodiversity caused by the alterations of ecosystems loop back into these systems, by changing the ecosystem functions biodiversity provides (Chapin et al. 2000, Cardinale et al. 2012, Hooper et al. 2012). In this thesis, I investigated disturbance of tropical forests by human farming activities in Belize (Chapter 1) and fragmentation of woody habitats in landscapes dominated by farmland in Switzerland (Chapters 3 and 5). Disturbance was investigated as driver of biodiversity (Chapter 1) and fragmentation as driver of biodiversity and ecosystem functions (Chapters 3 and 5). Taxonomy of two wasp families was studied in farmland and forest of Belize (Chapter 2). I participated in a global research project on the relative importance of two groups of organisms in providing an ecosystem function (Chapter 4).

Habitat disturbance

Alteration of natural habitats by humans is a major driver of biodiversity loss. Increased anthropogenic disturbance in agricultural landscapes often leads to declines in species diversity (Tilman 1999, Kremen et al. 2002, Tscharntke et al. 2005, Chacoff and Aizen 2006, Tscharntke et al. 2012). However, the response of biodiversity to disturbance differs depending on the level of disturbance. An intermediate level of disturbance (close to natural disturbance levels) may cause positive effects on biodiversity (Connell 1978, Molino and Sabatier 2001), raising the expectation that environmental-friendly farming practices may allow for both production and biodiversity conservation, simultaneously (Perfecto and Vandermeer 2010). Sensitivity of biodiversity to disturbance also differs among taxa (Barlow et al. 2007), depending on species traits such as trophic level (Holt et al. 1999, Cagnolo et al. 2009). This underlines the necessity to study multiple taxa from different trophic levels. I studied the effect of habitat disturbance by land modification on biodiversity at three trophic levels in forested landscapes in Belize (Chapter 1).

Habitat fragmentation

Biodiversity and ecosystem services are not only affected by local drivers, such as local habitat disturbance, but also by the availability of resources at the landscape scale (Tscharntke et al. 2005, Kremen et al. 2007, Bengtsson 2010). Landscape effects can be mediated through the loss and/or

fragmentation of habitats providing resources (Hadley and Betts 2012, Tschardt et al. 2012). In real landscapes, habitat loss and fragmentation are often correlated, making it difficult to study these effects independently (Fahrig 2003). Here, thirty experimentally created study sites each consisting of seven young cherry trees on strips of permanent grassland helped to disentangle effects of habitat loss at the landscape scale and patch isolation as a measure of habitat fragmentation (Chapters 3 and 5).

Measuring biodiversity

Biodiversity is the variety of life, namely variation in genes, species, functional traits, biotic interactions and ecosystems (Magurran 2007, Cardinale et al. 2012). A community of species at a given location and scale can be characterised by the number of species (species richness), the number of traits (trait richness), the number of individuals (abundance) per species, per trait, or in total, the equitability between species (evenness), or with different biodiversity indices such as Shannon or Simpson, that incorporate richness and abundance into a single measurement of diversity (Magurran 2007, Tuomisto 2011, Cardinale et al. 2012). Several of these descriptors are involved in each other. For example, higher total abundance in a sample of a community is often correlated with higher species richness (Magurran 2007). Therefore, statistical tools, such as species accumulation curves, are often necessary to appropriately describe a community (Gotelli and Colwell 2001; Chapter 1). Furthermore, species diversity can be described at different scales: as mean number of species per local site (alpha diversity), as total number of species in a region (gamma diversity), and as variation in species among sites within the region (beta diversity) (Whittaker 1972, Anderson et al. 2011; Chapter 1). Species classification (taxonomy) is a fundamental prerequisite for ecological research with diverse communities in real landscapes (Swiss Academy of Sciences 2007, Smith et al. 2011). I collaborated with specialists of three different hymenopteran families for descriptions of new species, elaboration of new determination keys and species lists for Belize (Lohrmann et al. 2012; Chapter 2).

Ecosystem functions

Ecosystem functions are processes that control fluxes of energy or matter in an ecosystem (Cardinale et al. 2012). These functions may be delivered by organisms that depend on multiple and spatially segregated resources in the landscape (Kremen et al. 2007). Therefore, the effectiveness of ecosystem functions at a given location depends not only on local conditions but also on the configuration and composition of the landscape surrounding this location. I determined local (e.g. flower density, soil nitrogen) and landscape drivers (e.g. habitat loss and isolation) of two ecosystem functions, namely pollination (Chapter 3) and suppression of herbivores by natural enemies (Chapter 5). If ecosystem functions provide benefits to humans they are referred to as ecosystem services (Cardinale et al. 2012). Pollination of crops is such an ecosystem service provided by both diverse communities of wild insects and domesticated honey bees. In a collaborative global research project, I helped understanding the relative importance of domesticated versus wild pollinators for crop production (Chapter 4).

Chapter 1:

High bee and wasp diversity in a heterogeneous tropical farming system compared to protected forest

Information

This chapter was published open source on 26 December 2012:

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Author contributions: CS and MHE designed experiment, CS and SR performed experiment, CS and MHE analysed data and wrote manuscript.

Legal note: Sampling of bees and wasps for this study in Belize was conducted under a mission for Civil Service Switzerland and is therefore not allowed to be considered as part of the dissertation.

Abstract

It is a globally important challenge to meet increasing demands for resources and, at the same time, protect biodiversity and ecosystem services. Farming is usually regarded as a major threat to biodiversity due to its expansion into natural areas. We compared biodiversity of bees and wasps between heterogeneous small-scale farming areas and protected forest in northern coastal Belize, Central America. Malaise traps operated for three months during the transition from wet to dry season. Farming areas consisted of a mosaic of mixed crop types, open habitat, secondary forest, and agroforestry. Mean species richness per site (alpha diversity), as well as spatial and temporal community variation (beta diversity) of bees and wasps were equal or higher in farming areas compared to protected forest. The higher species richness and community variation in farmland was due to additional species that did not occur in the forest, whereas most species trapped in forest were also found in farming areas. The overall regional species richness (gamma diversity) increased by 70% with the inclusion of farming areas. Our results suggest that small-scale farming systems adjacent to protected forest may not only conserve, but even favour, biodiversity of some taxonomic groups. We can, however, not exclude possible declines of bee and wasp diversity in more intensified farmland or in landscapes completely covered by heterogeneous farming systems.

Key words

Biotic homogenization, disturbance tolerance, forest conservation, habitat heterogeneity, species turnover, tropical agriculture

Introduction

IMPORTANCE OF MODIFIED LAND FOR BIODIVERSITY CONSERVATION

Although a considerable amount (>13%) of the world's terrestrial surface is nowadays designated as nationally or internationally protected areas (Coad et al. 2009) the effectiveness of protected areas in biodiversity conservation is limited, especially in the tropics: First, financial support for basic management activities to stop illegal and harmful human activities within parks is often lacking (Bruner et al. 2001). Second, about 12% of terrestrial vertebrates, mostly endemics, are not covered within the current protected area network (Rodrigues et al. 2004). And third, the long-term effectiveness of reserves depends strongly on human population density and activities in the surroundings (Wittemyer et al. 2008). Thus, more recently research on biodiversity conservation in the tropics has moved away from strictly focussing on protected areas (Soulé and Sanjayan 1998) to considering also the importance of anthropogenic habitats within a landscape mosaic (Tscharntke et al. 2005, Barlow et al. 2007, Chazdon et al. 2009, Gardner et al. 2009). This change of focus is crucial when taking into account increased competition for land, due to both increasing demands of resources (caused by human demography and wealth) and, at the same time, increasing loss of agricultural land due to climate change and urbanisation (Godfray et al. 2010).

EFFECTS OF HUMAN LAND-MODIFICATIONS ON BIODIVERSITY

The 'intermediate disturbance hypothesis' postulates maximum diversity at intermediate regimes of disturbance (Connell 1978). Although the validity of the underlying mechanisms is currently discussed (Fox 2012), this hypothesis has been widely tested in marine (Svensson et al. 2007) and forest ecosystems (Molino and Sabatier 2001), and can be applied to agricultural systems (Bruggisser et al. 2010). Increased anthropogenic disturbance in agricultural landscapes generally leads to declines in species diversity (Tilman 1999, Kremen et al. 2002, Tscharntke et al. 2005, Chacoff and Aizen 2006, Tscharntke et al. 2012). However, if land modification is moderate and leads to a more heterogeneous landscape it can also increase biodiversity (Andren 1994, Brown 1997, Tscharntke et al. 2005, Vulliamy et al. 2006, Winfree et al. 2007a). It remains an important question to what extent natural habitats can be modified without decreasing diversity (Scales and Marsden 2008, Godfray 2011) or, rephrased, how many species from natural habitats are retained in modified habitats with a certain level of disturbance (Gardner et al. 2009). In this study, we investigated a small-scale farming system with heterogeneous land-use practices embedded in a tropical forest landscape.

SPATIAL AND TEMPORAL COMMUNITY VARIATION (BETA DIVERSITY)

Spatial heterogeneity within one habitat type can lead to high variation of community composition between study sites (Duivenvoorden et al. 2002, Tuomisto et al. 2003, Kessler et al. 2009). If spatial heterogeneity is higher in a natural compared to a modified habitat, focussing on mean species richness per site can lead to serious underestimation of the conservation value of the more natural

habitat. Therefore, several authors emphasize the value of reporting community variation (beta diversity) over the whole study area (Basset et al. 2008, Scales and Marsden 2008, Kessler et al. 2009, Tscharrntke et al. 2012). Furthermore, habitat loss and land-use change can lead to the dominance of disturbance-tolerant generalist species (Warren et al. 2001) and thus increase the similarity of communities (effects on bees (Dormann et al. 2007), on plants (Vellend et al. 2007), on bees and wasps (Tylianakis et al. 2005)). The same is true for temporal heterogeneity: Strong temporal heterogeneity in biodiversity of a more natural habitat can lead to a serious underestimation of its conservation value, if sampling is temporally restricted to one season (Summerville and Crist 2005, Tylianakis et al. 2005). In this study, we collected insects over a spatiotemporal climatic gradient and included beta diversity in our analysis (see ‘Materials and Methods’).

CONSERVATION RESEARCH ON ARTHROPODS

Despite their overriding diversity and their importance for humankind through providing ecosystem services such as pollination or pest control (Ehrlich and Ehrlich 1992, Klein et al. 2007, Kremen et al. 2007), arthropods are widely neglected in conservation policies (Cardoso et al. 2011). However, conservation efforts based on other taxa, such as plant or vertebrates, are often inappropriate for arthropods because of low cross-taxon congruence (Barlow et al. 2007, Dormann et al. 2007, Gardner et al. 2009, Kessler et al. 2009, Axmacher et al. 2011). Effective conservation science therefore needs to incorporate more arthropod research (Scales and Marsden 2008). Within arthropods, responses to habitat modification may depend strongly on life-history traits of species. Predators and parasitoids of higher trophic levels may be more strongly affected by land modification than their hosts or prey (Davies et al. 2000, Tscharrntke et al. 2002, Cagnolo et al. 2009, Bailey et al. 2010, Schüepp et al. 2011). Therefore, we investigated three trophic groups of bees and wasps (Insecta: Hymenoptera): Bees (Apidae, Colletidae, Halictidae, Megachilidae) are important pollinators of wild and crop plants (Klein et al. 2007, Kremen et al. 2007). Paper wasps (Vespidae) predate on insects and play a role in biological pest control (Hanson and Gauld 1995). Spider wasps (Pompilidae) are secondary carnivores (fourth to higher trophic level) by using spiders as larval food (Hanson and Gauld 1995). Besides trophic level, degree of sociality and nesting requirements in arthropods may influence the susceptibility to habitat modification (Klein et al. 2003, Brosi et al. 2008, Ricketts et al. 2008, Jha and Vandermeer 2010, Potts et al. 2010). If species with different life-history traits are not analysed separately, effects of land modification may be masked by opposite reactions. Here, we analysed separately the three trophic groups mentioned above and controlled for opposing effects of different degrees of sociality and nesting requirements in bees.

HYPOTHESES

The main goal of this study was to quantify the impact of farming areas on biodiversity. In contrast to previous studies, we selected farming areas embedded in a landscape with a high proportion of

protected forest and low level of anthropogenic disturbance. We focussed on three groups of bees and wasps at different trophic levels, of which two (paper and spider wasps) are very rarely used in biodiversity assessments, and for which human impact through land modification is basically unknown. Because farming areas were relatively small and heterogeneous in their land-use practices, we expected higher diversity (richness, abundance and evenness) of bees and wasps in farming areas. We further tested if different degrees of sociality and nesting requirements in bees lead to different responses to land modification. Finally, we hypothesized a higher spatiotemporal community variation (beta diversity) in forest compared to farmland because of naturally occurring heterogeneity between forest sites in the northeast and southwest of our study region (changes in forest structure and plant community; see section ‘Study Area’ in ‘Materials and Methods’).

Materials and methods

ETHICS STATEMENT

Insects were collected and exported under the Belizean Forest Department research permit no. CD/60/3/09 (35), issued on November 9, 2009. Additionally, we got oral or written approvals for insect sampling from all private land owners (eight farmers and two owners of private protected areas). Bees and wasps are not legally protected in Belize.

STUDY AREA

The study was conducted in northern coastal Belize, Central America, south and west of the village Sarteneja in Corozal District (N 18°12’-18°20’ / W 88°07’-88°16’). The study sites were spread over an area of about 400 km² and along a climatic gradient from dry and hot ‘Yucatecan low semi-deciduous forest’ in the northeast to cooler and more humid ‘Yucatecan medium-sized semi-evergreen forest’ and ‘*Cohune*-palm dominated forest’ in the southwest (Bijleveld 1998). All forest types were relatively dry, low in stature, and seasonal as compared to most of Central America. Besides forest, the main habitat types of the area were savannah, brackish water lagoons, mangroves, some human settlements, and small-scale farming areas. Mean annual rainfall ranged from approx. 1500 mm in the north to 2000 mm in the west and south (Meerman and Clabaugh 2010) and mean temperature during the study period differed between 24.3°C in the north and 22.3°C in the west and south (measured using DS1923 Hygrochron iButtons, Maxim, Sunnyvale, USA).

STUDY SITES

Both the study sites in the forest (seven sites) and in small scale farming areas (eight sites) were equally distributed over the entire study area and along the whole climatic gradient of the study area (Fig. S1). Forest and farming sites were interspersed to avoid problems of spatial autocorrelation. Five out of the seven study sites in forest lay within the protected area of Shipstern Nature Reserve (www.shipstern.org), one lay within a smaller private reserve (www.wildtracksbelize.org), and one in

an unused forest close to the private land of the same organisation. Although forest sites were under protection for many years, in the past all of them were subject to some human disturbance (possibly including selective logging) and natural disturbance (hurricanes). Therefore we use the term ‘natural’ or ‘protected forest’ instead of ‘primary forest’. Forest sites were located between 120 and 140 m from the next forest edge of farmland or clearings for forest roads. Farming areas consisted of a mosaic of mixed crop types, open land, agroforestry, and secondary forest. Within the vicinity of traps in farmland, we monitored more than 30 species of crops. Most crops are grown for subsistence. However, some cash crops (e.g. plantain, banana, bean, and onions) are sold to local markets, and recently Mahogany trees were planted to sell to the international timber market. Farmland size ranged from 3-80 ha and conversion from forest into farmland took place 8-70 years ago. All farming areas were fully surrounded by natural forest. Traps in farming areas were set at least 100 m from the next natural forest edge. The mean distance between two study sites was 9.9 km (min: 440 m, max: 17 km). The minimum distance between two study sites of the same habitat type was 1.3 km.

TRAPPING METHODS

One Malaise trap (B&S Entomological Services, UK) was installed at each study site. Malaise traps are an efficient method for sampling flying insects (Campbell and Hanula 2007) and also adequate in tropical forest systems (Missa et al. 2009). Traps operated from December 2009 to February 2010, covering both the wet season with heavy rain falls in December and the beginning of the dry season in February. All traps were sampled weekly. Every second week a small container (6 x 5 x 5 cm) with orchid scents was hung into the Malaise trap to attract male orchid bees (Apidae: Euglossini), which are otherwise rarely collected (Roubik and Hanson 2004). Male orchid bees gather chemical compounds from orchids and other plant families and display them during courtship (Roubik and Hanson 2004). We used three of the most commonly used attractants: cineole, eugenol (each 0.4 ml / week), and methyl salicylate (0.8 ml / week). Scents constantly dispersed over one week through four small holes in the container (2 mm diameter each). Although, to our knowledge, negative (repellent) effects of attractants on non-orchid bee species has never been reported, we added scents to traps only every second week to avoid possible exclusion of some sensitive bee species. Whereas the presence of attractants had a very strong positive effect (almost hundredfold increase) on abundance of orchid bees (linear mixed effect model with scent as fixed and study sites as random factor: $p < 0.001$) it had no effect on the abundance of non-orchid bees (same model: $p = 0.17$). Because trapping efficiency of Malaise traps depend on vegetation structure the traps in farming areas were set up in locations characterised by understory vegetation and a closed canopy to mimic the same vegetation structure as in forest.

DETERMINATION OF BEES AND WASPS

Collected bees and wasps were either mounted (bees and spider wasps) or stored in 85% ethanol (paper wasps), and identified by specialists (see Acknowledgements). More than 88% of all individuals were determined to species level (72 species). The remaining samples were assigned to morphospecies (36 morphospecies) because revisions of many neotropical bee and wasp genera are still lacking. Hereafter, morphospecies and species are referred to simply as *species*. Bees were assigned to four groups of sociality (solitary, social, eusocial, and cleptoparasitic) and three group of nesting requirements (cavity-nesting, ground-nesting, and wood-nesting) (Hanson and Gauld 1995, Michener 2007, Calvillo et al. 2010, Jha and Vandermeer 2010) (Table S1). ‘Social’ comprised all live forms between strictly solitary and eusocial, namely communal, semisocial, and primitively eusocial. Bees in the genera *Augochlora*, *Ceratina*, *Euglossa*, and *Lasioglossum* were classified as social, although this is not certain for every species. Nesting of cleptoparasitic bees was defined according to the nests of their hosts. All collected specimens, except some vouchers, are archived in the Natural History Museum of Bern, Switzerland (Naturhistorisches Museum der Burgergemeinde Bern).

STATISTICAL ANALYSIS

Differences in species richness and abundance between forest and farming areas were analysed using Generalized Linear Models (GLM) for overdispersed count data (quasi-poisson errors with a log link function), and differences in Simpson’s Evenness $E_{1/D}$ (Smith and Wilson 1996) were analysed using non-parametric Wilcoxon rank sum test because residuals could not be normalised with any transformation. Because the observed number of species is sensitive to the number of individuals sampled (Colwell et al. 2012) we performed individual-based rarefaction curves, using the open source software EstimateS 8.2.0 (Colwell 2009). Forest and farmland were compared using sample-based rarefaction curves, where individuals were set as samples (Barlow et al. 2007). Rarefaction curves and 95% confidence intervals were calculated using Mao Tau estimator. Significance (at $p < 0.05$) was inferred if the total observed richness of the habitat with the smaller sample (habitat type with lower number of individuals) fell outside the confidence interval of the larger sample.

To determine temporal community variation (temporal beta diversity) we performed additive partitioning of species diversity (Lande 1996), using spatial replication (study sites) and temporal variation (weeks) (Tylianakis et al. 2005). Two major criticisms exist against additive partitioning: First, beta diversity is not independent of alpha, thus formulating a problem if alpha diversities of compared habitats are very different (Jost 2007). Second, the measure of additive beta diversity loses its resolution for datasets with many samples sharing few species (Anderson et al. 2011). We consider these limitations of minor importance for the current study, because alpha diversity of forest and farmland were within the same order of magnitude and because a considerable number of species were shared between samples. Because in additive partitioning spatial beta diversity is not replicated and therefore not testable, we instead compared homogeneity of multivariate dispersions between forest

and farmland based on Sørensen (presence/absence) and Bray-Curtis (abundance included) dissimilarities (Method V4 in (Anderson et al. 2011)). Differences in temporal species variation (additive partitioning) and spatial homogeneity of multivariate dispersions between forest and farmland were tested using Generalised Least Squares Models (GLS), taking into account heterogeneity of residual variances (Zuur 2009). Diagnostic plots of GLS indicated normal distribution of residuals. Apart from rarefaction curves, all analyses were carried out in the open source software R 2.12.2 (R Development Core Team 2012), using the packages *vegan* (Oksanen et al. 2011) and *nlme* (Pinheiro et al. 2012).

Results

LOCAL (ALPHA) DIVERSITY

In total, 1133 bees of 43 species, 720 paper wasps of 19 species and 1288 spider wasps of 46 species were collected (Table S1). Species richness of paper wasps was higher in farming areas compared to protected forest ($t_{1,13} = 2.43$; $p = 0.030$) and bees showed a trend in the same direction ($t_{1,13} = 2.01$; $p = 0.066$) (Fig. 1A). Species richness of spider wasps was not significantly different between farming areas and forest ($t_{1,13} = 0.88$; $p = 0.40$). The higher species richness in farming areas was largely due to species trapped in farmland that did not occur in the forest. Conversely, a high percentage of species trapped in forest was also found in farming areas (72% of bees, 85% of paper wasps, and 77% of spider wasps) (Fig. 2). Abundance did not differ significantly between forest and farmland in any of the three groups (bees: $t_{1,13} = 1.50$; $p = 0.16$; paper wasps: $t_{1,13} = 1.95$; $p = 0.073$; spider wasps: $t_{1,13} = -1.39$; $p = 0.19$; Fig. 1B). Simpson's evenness of paper wasps was significantly higher in farming areas than in forest ($W_{7,8} = 53$; $p = 0.002$), but bees and spider wasps did not differ between habitat types (bees: $W_{7,8} = 40$; $p = 0.19$; spider wasps: $W_{7,8} = 34$; $p = 0.54$; Fig. 1C). Rarefaction curves show higher species richness in farmland for bees and spider wasps but not for paper wasps (Fig. S2). Bees showed consistently higher species richness and abundance in farming areas compared to forest in all degrees of sociality and nesting requirements (Fig. 3). Overall species richness (gamma diversity) was 70% higher in farmland (Fig. 4A-C, gamma diversity indicated by total height of bars).

COMMUNITY VARIATION (BETA DIVERSITY)

Bees and paper wasps showed a trend towards higher temporal community variation (beta diversity) in farmland compared to forest (bees: $t_{1,13} = 1.96$; $p = 0.072$; paper wasps: $t_{1,13} = 1.85$; $p = 0.087$; Fig. 4A,B). Temporal community variation of spider wasps did not show a significant pattern ($t_{1,13} = 1.56$; $p = 0.139$; Fig. 4C). Spatial community variation (beta diversity) based on presence/absence data (Sørensen) was significantly higher in farmland for wasps (paper wasps: $t_{1,13} = 5.40$; $p < 0.001$; spider wasps: $t_{1,13} = 2.67$; $p = 0.019$; Fig. 4E,F) but this trend was not statistically significant for bees ($t_{1,13} = 1.87$; $p = 0.085$; Fig. 4D). Spatial community variation (beta diversity) based on abundance data

(Bray-Curtis) did not differ between forest and farmland in any of the three taxa ($|t_{1,13}| < 1.15$; $p > 0.269$; Fig. 4G-I).

Discussion

LOCAL (ALPHA) DIVERSITY

Our results based on linear models and rarefaction curves suggest that small-scale farming systems do not only conserve but even favour biodiversity of some taxonomic groups. Species richness of bees and wasps was higher in farmland areas, first because most species occurring in adjacent forest were also found within farmland, and second because many exclusive species inhabited farmland that were not trapped in forest (Fig. 2). In other words, the proportion of species trapped in forest inhabiting or using farmland was high, indicating the compatibility of this farming system with bee and wasp conservation (Gardner et al. 2009). The studied farmland type matches perfectly the description of favourable agriculture for pollinators by Kremen (Kremen 2008): "Positive effects of agriculture on pollinator communities may be more likely to occur in regions in which the presence of agriculture increases habitat heterogeneity, such as farming landscapes that include relatively small field sizes, mixed crop types within and between fields, and patches of noncrop vegetation, such as hedgerows, fallow field, meadows, and seminatural wood or shrublands". In our study region, a natural forest matrix surrounded the small-scale farming areas within dispersal and foraging distance of investigated bees and wasps. Because distance to natural habitat strongly decreases richness and abundance of bees (Chacoff and Aizen 2006, Ricketts et al. 2008) it remains unclear to what extent species trapped in forest may maintain viable populations in landscapes covered completely by these farmland habitats (Chazdon et al. 2009). Even if bee and wasp species richness was equal or higher within farmland, and most species trapped in forests were also found in farming areas, forest may nevertheless be a vital component within the life cycle of some or many of the species and may serve as constant source for colonisation of farmland. In accordance with our results, two studies on plants, vertebrates and invertebrates showed that a considerable number of forest species persist in secondary forest, agroforestry, and even pastures if the surrounding landscape comprises high amounts of mature forest (Gascon et al. 1999, Pardini et al. 2009).

In addition to the desirable features of the studied agricultural system, bees and wasps in tropical forest may be less sensitive to human disturbance compared to other taxa (Barlow et al. 2007, Kessler et al. 2009). This emphasises that our results cannot be generalised to other taxa. At least, in our study effects of land modification were more or less consistent between investigated groups of bees and wasps. The same was true in a study on bees and wasps in Ecuador (Tylianakis et al. 2006). Furthermore, all groups of sociality and nesting requirements in bees were positively affected by land modification (Fig. 3), in contrast to previous findings where effects of habitat types or levels of disturbance on bee communities depended on life history traits (Klein et al. 2003, Brosi et al. 2008, Jha and Vandermeer 2010).

COMMUNITY VARIATION (BETA DIVERSITY)

In contrast to our hypothesis, spatial community variation (beta diversity) of bees and wasps was equal or higher in farming areas compared to forest (Fig. 4A-F). High beta diversity within a study region can be a statistical artefact due to low local alpha diversity (Karp et al. 2012). However, in our study we can exclude such an inflation of beta diversity because both alpha and beta diversity were increased in farmland. Habitat heterogeneity is a major driver of community variation (Duivenvoorden et al. 2002, Tuomisto et al. 2003, Kessler et al. 2009). Thus, differences in farming areas due to variable land-use practices could have led to higher beta diversity in farmland. High management diversity between different agroforestry plots within a study region appeared to be responsible for high beta diversity of bees in Indonesia (Hoehn et al. 2010). Spatial community variation disappeared when analyses were performed including abundances (Fig. 4G-I), showing that effects of beta diversity were driven by the high percentage of species with very low abundances (29% of species are singletons). Temporal community variation of bees and paper wasps tended to be higher in farmland than in forest, in contrast to a study in Ecuador (Tylianakis et al. 2005) where lower temporal beta diversity was found in more disturbed habitat types. However, in that study lower beta diversity occurred only in open habitat types, whereas we compared protected forest against a farming system consisting of a considerable amount of woody habitat. In conclusion, the increase in the regional species pool (gamma diversity) by 70% through species only occurring in farming areas (Fig. 4A-C) was composed of both, higher local diversity (alpha) and higher spatial and temporal community variation (beta diversity).

EFFECTS OF HUMAN DISTURBANCE ON BEES AND WASPS

We found that species richness of bees and wasps was favoured in farmland areas compared to protected forest and we conclude that bees and wasps occurring in natural forest were not susceptible to the extent and disturbance level of the studied farming system (Gardner et al. 2009). Our results are in line with the ‘intermediate disturbance hypothesis’ (Connell 1978) predicting higher biodiversity at higher levels of disturbance in generally undisturbed, relatively natural landscapes. Farming areas create additional habitats and benefit biodiversity through increased heterogeneity of resources within foraging distance (Andren 1994, Eltz et al. 2002, Benton et al. 2003, Tscharntke et al. 2005, Jha and Vandermeer 2010). To the extreme, disturbed areas may even lead to a spillover of rich farmland bee communities into forest remnants (Hagen and Kraemer 2010, Schleuning et al. 2011). However, this may not necessarily be beneficial considering the competitive advantage of some abundant generalist farmland species. The resilience of forest bees to disturbance may hold as long as some elements of native habitats remain in the disturbed areas (Samejima et al. 2004, Brosi et al. 2008). However, in very intensively managed landscapes, additional disturbance leads to a reduction of diversity (Kremen et al. 2002, Tscharntke et al. 2005). Due to the presence of naturally occurring disturbance in Belizean forests caused by hurricanes, forest communities may be less sensitive to disturbance by logging, as proposed for butterflies by Lewis (Lewis 2001).

From a conservation perspective, it is debatable if species inhabiting modified habitats but not occurring in native forest are of high concern. Disturbed areas may be first invaded by disturbance-tolerant widespread or even non-native generalist species, which are of low conservation value (Brown 1997, Barlow et al. 2007). These species may become dominant components in communities of disturbed habitats. In Britain, continuing habitat degradation led to an increased dominance of generalist butterfly species (Warren et al. 2001). The lower Simpson's Evenness of paper wasps in farmland compared to forest reflects the high dominance (Magurran 2007) of the most abundant species in farming areas, namely *Polybia occidentalis nigratella* (Table S1). However, this species is also the most abundant species in forest and it is still an open research question how important community evenness is for ecosystem functioning (Tscharntke et al. 2012). Comprehensive comparisons of the biogeography and conservation value of species between farming areas and forest are not possible in our study due to lack of sound information on species distributions, rarity, and specialisation, and because some individuals could only be determined to morphospecies.

Conclusions

Our results show that agricultural systems exist, where local (alpha) diversity and variation in communities (beta diversity) are similar or higher than in protected forest and where species occurring in forests also use these farmlands. We conclude that heterogeneous and small-scale farming areas embedded in a matrix of protected forest are compatible with biodiversity conservation for some taxonomic groups. However, it remains unclear to what extent these systems would retain forest species if protected forest in the surrounding was further reduced or if existing farmland areas are further intensified. Finally, we do not conclude that a transfer of forest into heterogeneous small-scale farming systems is desirable. But, if necessary to meet demands of local populations, it can be tolerated from the perspective of bee and wasp conservation.

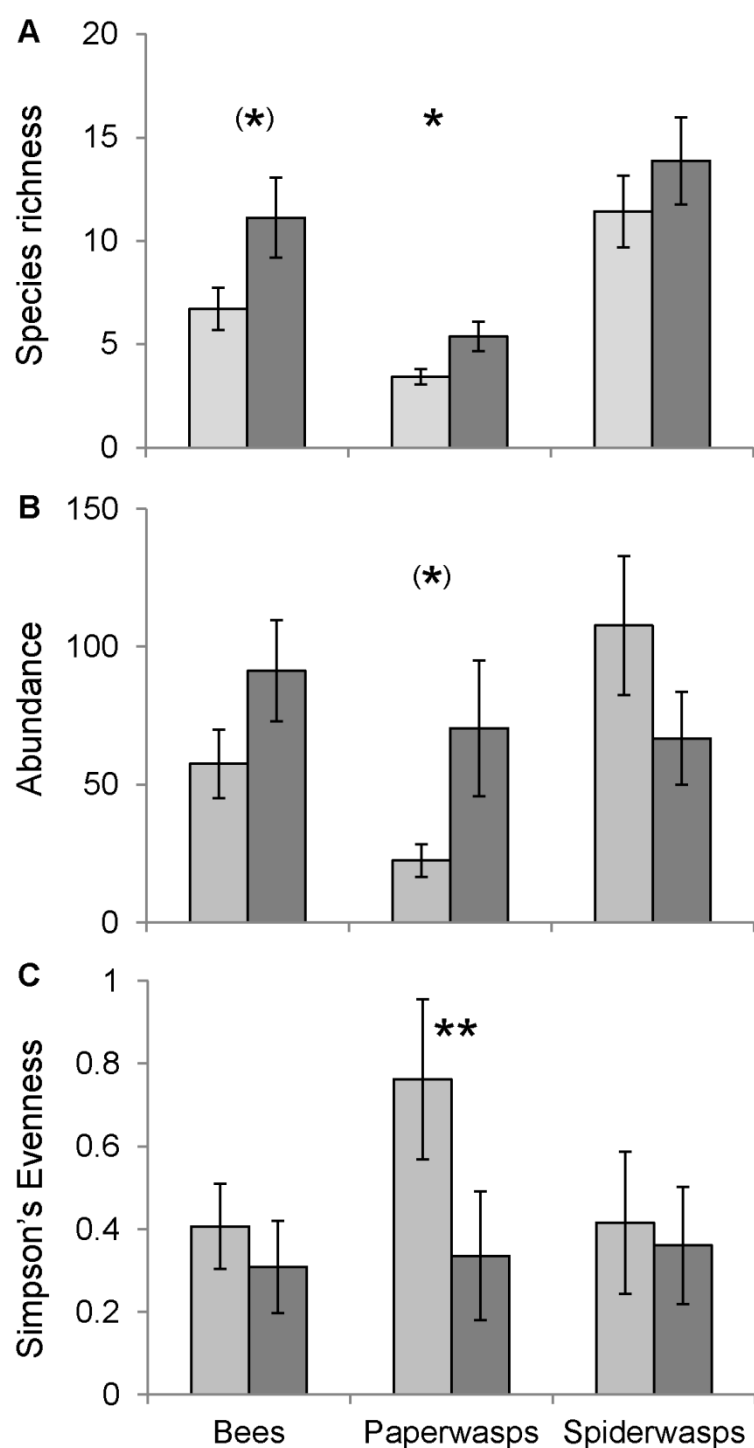
Figures

Figure 1. Biodiversity of bees and wasps. Differences in (A) species richness (mean no. of species per study site), (B) abundance (mean no. of collected individuals per site), and (C) Simpson's Evenness per site for bees, paper wasps, and spider wasps between protected forest (light grey) and heterogeneous farmland (dark grey). Error bars show standard error of the mean. Significance levels: ** p < 0.01, * p < 0.05, (*) p < 0.1.

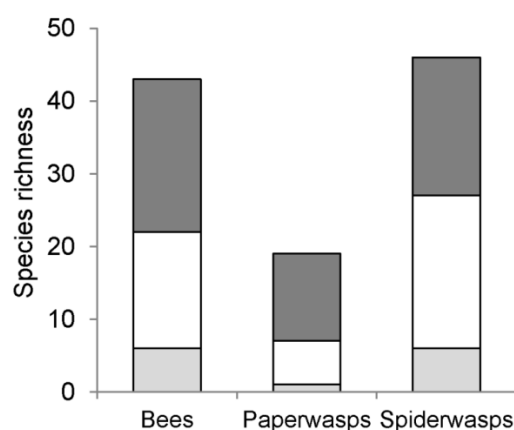


Figure 2. Exclusive and shared species across habitat types. Pooled species richness (over 3 months and 15 study sites) of bees, paper wasps, and spider wasps exclusively trapped in protected forest (light grey), in heterogeneous farmland (dark grey), and trapped in both habitat types (white).

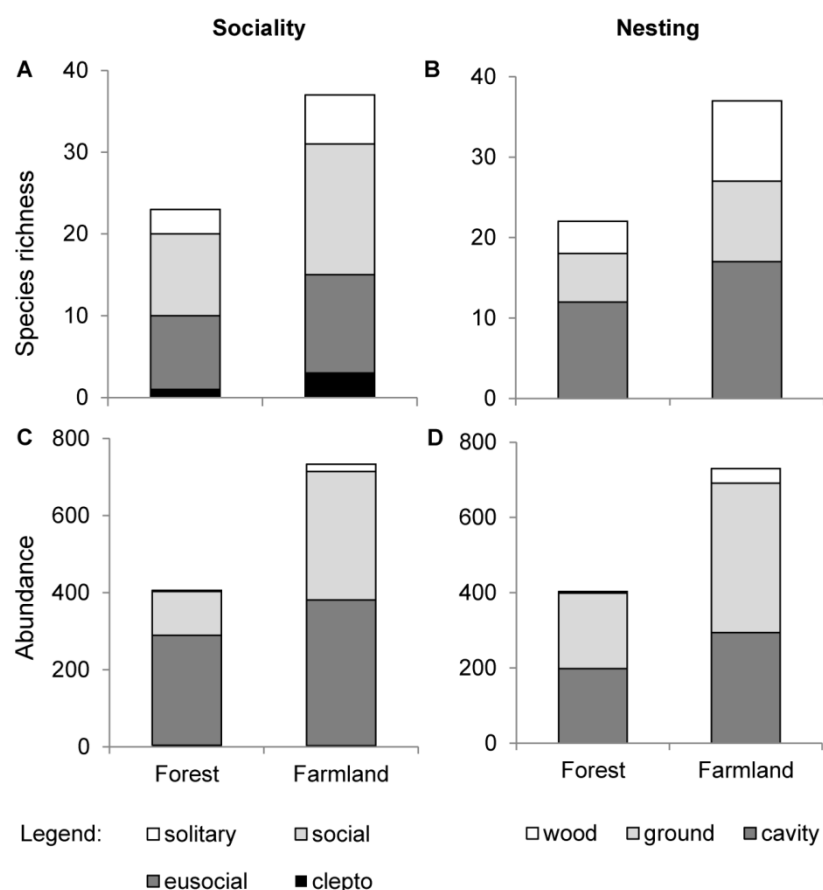


Figure 3. Degree of sociality and nesting requirements in bees. Differences in (A, B) species richness and (C, D) abundance of bees between protected forest and heterogeneous farmland (pooled data over 3 months and 15 study sites). Bees are separated into four degrees of sociality (solitary, social, eusocial, and cleptoparasitic) and three groups of nesting requirements (wood-nesting, ground-nesting, cavity nesting). For assignment of bees see Table S1.

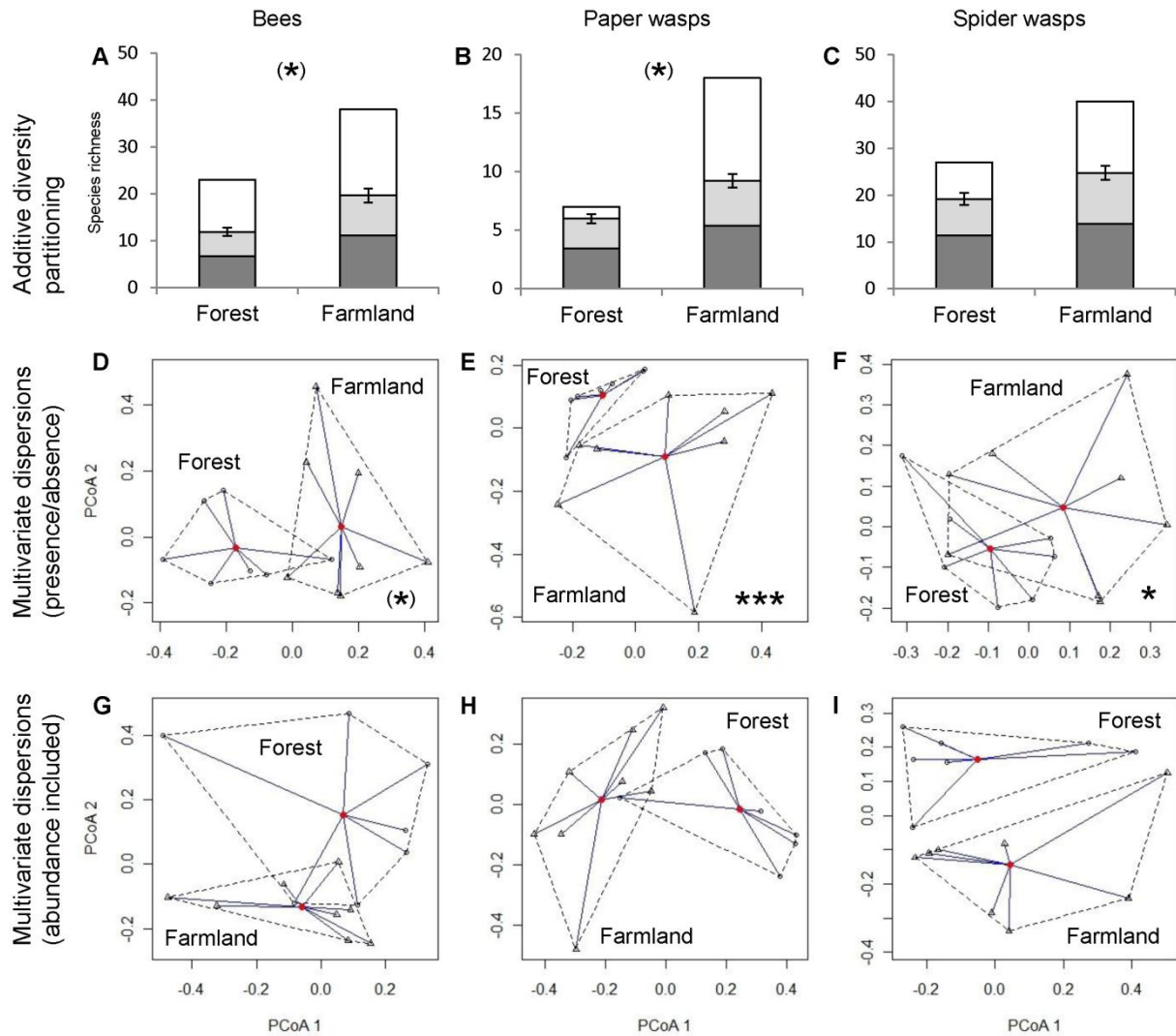


Figure 4. Community variation (beta diversity) of bees and wasps. (A-C) Alpha diversity (dark grey), temporal beta diversity (light grey), and spatial beta diversity (white) compared between protected forest and heterogeneous farmland based on additive diversity partitioning. Temporal beta diversity was replicated and statistically tested. Error bars show standard error of the mean. Total height of bars indicates overall (gamma) diversity within forest or farmland. (D-I) Spatial beta diversity, measured as distance to centroid (homogeneity of multivariate dispersions), was based on (D-F) Sørensen dissimilarities (presence/absence) and (G-I) Bray-Curtis dissimilarities (abundance included). Points (forest) and triangles (farmland) represent species composition of one study site. Larger distances between study sites and the mean composition of a habitat type (unbroken lines) indicate higher difference in species composition. Dashed lines connect all sites of one habitat type. Significance levels: *** $p < 0.001$, * $p < 0.05$, (*) $p < 0.1$.

Supporting information



Figure S1. Study area. Google Earth map (Google 2011) showing the study area in northern Belize, Central America. Study sites are located in heterogeneous, small-scale farmland (n=8) and in protected forest (n=7).

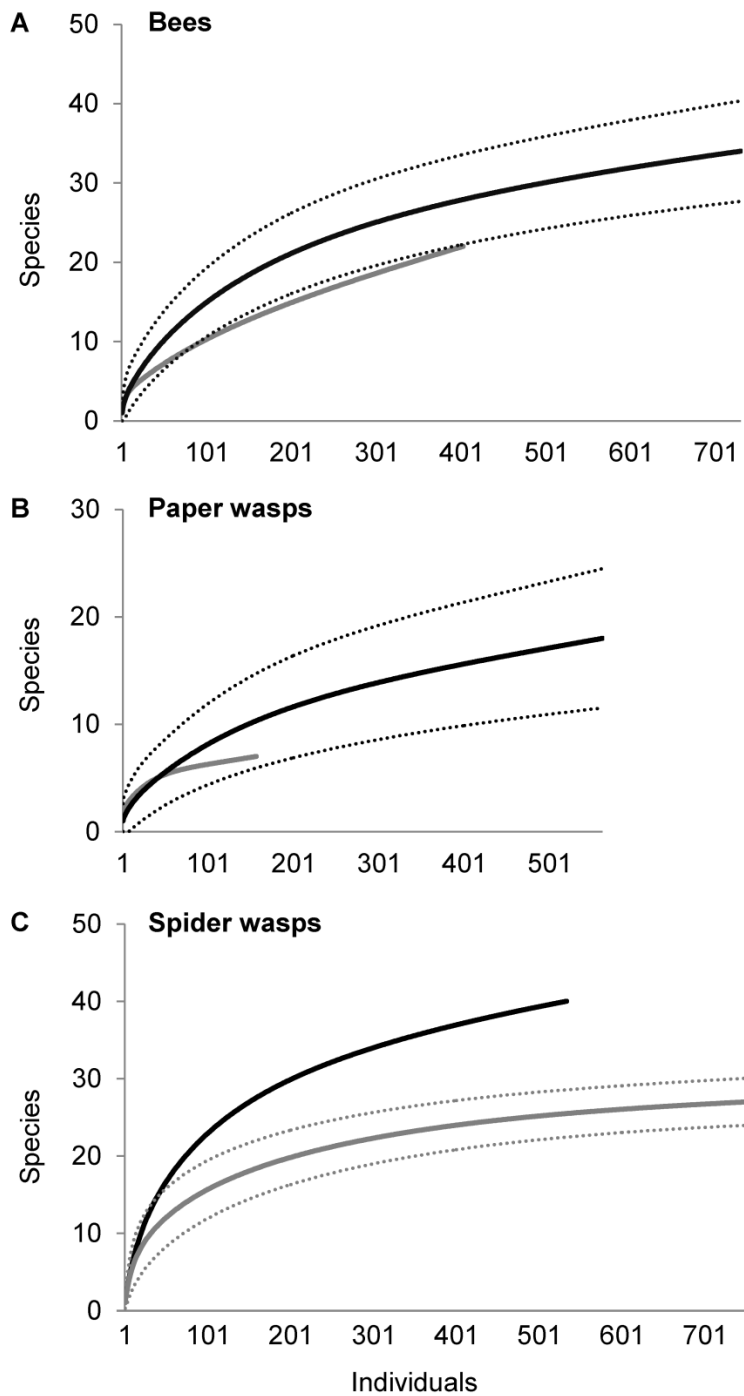


Figure S2. Individual-based rarefaction curves. Solid lines are rarefaction curves for (A) bees, (B) paper wasps, and (C) spider wasps in protected forest (grey) and heterogeneous farmland (black) and dotted lines are 95% confidence intervals for the larger sample, i.e. the habitat type with the higher total amount of individuals (see ‘Materials and Methods’ for details).

Table S1. Species list with total abundances in forest (n=7) and farming areas (n=8).

| Family | Tribe | Genus | Species | LHT ¹ | Forest | Farmland | | |
|--------------|---------------------------------------|----------------------------------------------|----------------------------------------------|-------------------------------------|--------------------------------------|----------|-----|---|
| Apidae | Apini | <i>Apis</i> | <i>mellifera</i> Linnaeus, 1758 | eus, c | 1 | 24 | | |
| | Ceratinini | <i>Ceratina</i> (<i>Calloceratina</i>) | <i>cf regalis</i> Cockerell, 1912 | soc, w | | 7 | | |
| | | | <i>eximia</i> Smith, 1862 | soc, w | | 4 | | |
| | | | <i>viridicincta</i> Cockerell, 1931 | soc, w | | 5 | | |
| | | | <i>Ceratina</i> (<i>Zadontomerus</i>) | sp. | soc, w | | 7 | |
| | | | <i>Ceratina</i> (<i>Ceratinula</i>) | sp. | soc, w | 1 | | |
| | Epeolini | <i>Triepeolus</i> | sp. | cle, g | | 1 | | |
| | Eucerini | <i>Peponapis</i> (<i>Peponapis</i>) | <i>cf limitaris</i> (Cockerell, 1906) | sol, g | 1 | 5 | | |
| | Euglossini | <i>Euglossa</i> | <i>tridentata</i> Moure, 1970 | soc, c(e) | | 1 | | |
| | | | <i>variabilis</i> Friese, 1899 | soc, c(e) | 1 | 6 | | |
| | | | <i>viridissima</i> Friese, 1900 ² | soc, c | 91 | 222 | | |
| | | | <i>Exaerete</i> | <i>smaragdina</i> (Guérin-M., 1844) | cle, c(e) | 4 | | |
| | | | Exomalopsini | <i>Exomalopsis</i> | sp. | soc, g | | 1 |
| | | | Meliponini | <i>Cephalotrigona</i> | <i>zexmeniae</i> (Cockerell, 1912) | eus, c | | 1 |
| | | | | <i>Frieseomelitta</i> | <i>nigra</i> (Cresson, 1878) | eus, c | | 1 |
| | | | | <i>Lestrimelitta</i> | <i>niitkib</i> Ayala, 1999 | eus, c | 4 | 1 |
| | | | | <i>Melipona</i> | <i>beecheii</i> Bennett, 1831 | eus, c | 1 | 9 |
| | | | | <i>Nannotrigona</i> | <i>perilampoides</i> (Cresson, 1878) | eus, c | | 1 |
| | <i>Partamona</i> (<i>Partamona</i>) | <i>bilineata</i> (Say, 1837) | | eus, c | 2 | 5 | | |
| | <i>Plebeia</i> | <i>cf frontalis</i> (Friese, 1911) | | eus, c | 87 | 8 | | |
| | <i>Scaptotrigona</i> | <i>pectoralis</i> (Dalla Torre, 1896) | | eus, c | | 1 | | |
| | <i>Trigona</i> | <i>corvina</i> Cockerell, 1913 | | eus, c(e) | 1 | | | |
| | | | | <i>fulviventris</i> Guérin-M., 1844 | eus, g | 184 | 323 | |
| | | | <i>fuscipennis</i> Friese, 1900 | eus, c | 1 | 2 | | |
| | | <i>Trigonisca</i> | sp. | eus, c | 4 | 2 | | |
| | Osirini | <i>Osiris</i> | sp. | cle, w | | 1 | | |
| | Tapinotaspidini | <i>Paratetrapedia</i> (<i>Lophopedia</i>) | sp. | sol, w | 1 | | | |
| | | <i>Paratetrapedia</i> | sp. | sol, w | | 2 | | |
| | Colletidae | Caupolicanini | <i>Ptiloglossa</i> | sp. A | sol, g | | 3 | |
| | | | | sp. B | sol, g | | 1 | |
| Halictidae | Augochlorini | <i>Augochlora</i> (<i>Augochlora</i>) | <i>cf. nigrocyanea</i> Cockerell, 1897 | soc, w | | 5 | | |
| | | | sp. B | soc, w | 1 | | | |
| | | | sp. C | soc, w | 1 | 5 | | |
| | | | sp. D | soc, w | | 1 | | |
| | | <i>Augochlora</i> (<i>Oxystoglossella</i>) | sp. | soc, g | 1 | 14 | | |
| | | <i>Augochloropsis</i> (<i>Paraugo.</i>) | sp. | soc, g | 1 | 3 | | |
| | | <i>Caenaugochlora</i> (<i>Caenaugo.</i>) | sp. | soc, g | 3 | | | |
| | | <i>Megalopta</i> | <i>cf centralis</i> Friese, 1926 | soc, w | | 2 | | |
| | | <i>Pereirapis</i> | <i>semiaurata</i> (Spinola, 1851) | soc, g | | 4 | | |
| | Halictini | <i>Lasioglossum</i> (<i>Dialictus</i>) | sp. | soc, g | 11 | 42 | | |
| Megachilidae | Megachilini | <i>Coelioxys</i> (<i>Cyrtocoelioxys</i>) | sp. | cle, c(e) | | 1 | | |
| | | <i>Megachile</i> (<i>Chelostomoides</i>) | sp. | sol, c(e) | | 7 | | |
| | | <i>Megachile</i> (<i>Leptorachis</i>) | sp. | sol, c(e) | 1 | 2 | | |

¹ Life-history traits (LHT) of bees: eus = eusocial, soc = social, sol = solitary, cle = cleptoparasitic, c = cavity-nesting, g = ground-nesting, w = wood-nesting, (e) = potentially also building exposed nests. *Augochlora*, *Ceratina*, *Euglossa*, and *Lasioglossum* were classified as social, although this is not certain for every species. Nesting of cleptoparasitic bees was defined according to the nests of their hosts.

² potentially including cryptic sibling species *E. dilemma* Bembé & Eltz 2011

Table S1 (cont.)

| Family | Subfamily | Genus | Species | Forest | Farmland |
|------------|-------------|------------------------|-----------------------------------------|--------|----------|
| Pompilidae | Ceropalinae | <i>Ceropales</i> | <i>cubensis albopicta</i> Cresson, 1865 | | 8 |
| | | | <i>rugata</i> Townes, 1957 | | 2 |
| | Pepsinae | <i>Irenangelus</i> | <i>hispaniolae</i> Evans, 1969 | 4 | |
| | | <i>Ageniella</i> | <i>fabricii</i> Banks, 1944 | | 2 |
| | | | <i>maya</i> Banks, 1931 | 2 | 5 |
| | | | sp. A | 9 | 10 |
| | | | sp. D | | 1 |
| | | | sp. E | | 1 |
| | | | sp. G | | 1 |
| | | | sp. H | 1 | |
| | | | <i>thione</i> Banks, 1946 | 1 | 3 |
| | | | <i>utilis utilis</i> (Cameron, 1891) | 3 | 4 |
| | | <i>Auplopus</i> | <i>esmeralda</i> (Banks, 1925) | 2 | |
| | | | <i>gaumeri</i> Dreisbach, 1963 | 8 | 3 |
| | | | sp. B | 21 | 3 |
| | | | sp. C | | 1 |
| | | | sp. D | | 1 |
| | | <i>Caliadurgus</i> | <i>pruinus</i> (Dreisbach, 1961) | 1 | 6 |
| | | <i>Dipogon</i> | <i>moctezuma</i> Evans, 1999 | | 1 |
| | | <i>Minagenia</i> | sp. | 102 | 25 |
| | | <i>Priocnemella</i> | sp. B | 4 | 6 |
| | | | <i>tabascoensis</i> (Cameron, 1891) | 1 | 4 |
| | | <i>Priocnessus</i> | sp. | 5 | 1 |
| | Pompilinae | <i>Agenioideus</i> | <i>birkmanni</i> (Banks, 1910) | 5 | 10 |
| | | <i>Allaporus</i> | <i>smithianus</i> (Cameron, 1893) | 71 | 44 |
| | | <i>Anoplius</i> | <i>amethystinus</i> (Fabricius, 1793) | | 2 |
| | | | <i>cuaudemoc</i> Evans, 1966 | | 34 |
| | | | <i>decorus</i> (Cameron, 1893) | 3 | |
| | | | sp. | | 6 |
| | | <i>Aporinellus</i> | <i>medianus</i> Banks, 1917 | | 2 |
| | | | <i>yucatanensis</i> (Cameron, 1893) | | 1 |
| | | <i>Aporus</i> | <i>chiapanus</i> Evans 1966 | 74 | 41 |
| | | | <i>concolor</i> (Smith, 1860) | | 3 |
| | | | <i>idris idris</i> (Cameron, 1897) | 35 | 9 |
| | | | <i>notabilis</i> (Smith, 1960) | 15 | 7 |
| | | | <i>nigribasis</i> Banks, 1925 | 12 | 1 |
| | | <i>Episyron</i> | <i>cressoni</i> (Dewitz, 1881) | | 15 |
| | | <i>Notocyphus</i> | sp. B | 3 | 44 |
| | | | sp. C | 4 | |
| | | | <i>violaceipennis</i> Cameron, 1893 | 261 | 188 |
| | | <i>Poecilopompilus</i> | <i>mixtus</i> (Fabricius, 1794) | | 1 |
| | | <i>Priochilus</i> | <i>gracilis</i> Evans, 1966 | | 6 |
| | | | <i>splendidulus</i> (Fabricius, 1804) | 2 | |
| | | <i>Psorthaspis</i> | <i>formosa</i> (Smith, 1862) | 17 | 23 |
| | | | <i>variegata</i> (Smith, 1862) | 88 | 8 |
| | | <i>Tachypompilus</i> | <i>unicolor cerinus</i> Evans, 1966 | | 1 |

Table S1 (cont.)

| Family | Genus | Species | Forest | Farmland |
|----------|-------------------------|---------------------------------------------------|--------|----------|
| Vespidae | <i>Agelaia</i> | <i>areata</i> (Say, 1837) | 63 | 56 |
| | | <i>centralis</i> (Cameron, 1907) | 6 | 6 |
| | <i>Brachygastra</i> | <i>mellifica</i> (Say, 1837) | | 8 |
| | <i>Hypancistrocerus</i> | sp. | | 1 |
| | <i>Mischocyttarus</i> | <i>deceptus</i> (Fox, 1895) | | 3 |
| | | <i>melanarius</i> (Cameron, 1906) | | 5 |
| | | <i>mexicanus mexicanus</i> (Saussure, 1854) | 6 | 5 |
| | <i>Pachodynerus</i> | sp. | | 1 |
| | <i>Parachartergus</i> | <i>apicalis</i> (Fabricius, 1804) | | 1 |
| | | <i>aztecus</i> Willink, 1959 | | 1 |
| | | <i>instabilis</i> Saussure, 1853 | | 1 |
| | <i>Polistes</i> | | | |
| | <i>Polybia</i> | cf. <i>parvulina</i> | 1 | |
| | | <i>nigrina</i> Richards, 1978 | 5 | 5 |
| | | <i>occidentalis nigratella</i> (du Buysson, 1905) | 75 | 461 |
| | | <i>rejecta</i> (Fabricius, 1798) | | 1 |
| | | <i>simillima</i> Smith, 1862 | | 1 |
| | <i>Santamenes</i> | <i>novarae</i> (Saussure, 1867) | | 1 |
| | <i>Stenodynerus</i> | <i>farias</i> (Saussure, 1857) | 1 | 3 |
| | <i>Synoeca</i> | <i>septentrionalis</i> Richards, 1978 | | 3 |

Chapter 2:

Catalogue of Dryinidae and Sclerogibbidae of Belize, with description of two new species

Information

This chapter is a short version of a manuscript published open source on 14 June 2012:

Schüepp C., Olmi M. 2012. Catalogue of Dryinidae and Sclerogibbidae (Hymenoptera: Chrysidoidea) of Belize, with description of two new species. Zootaxa 3346: 51–63.

Free download under: <http://www.mapress.com/zootaxa/2012/f/zt03346p063.pdf>

Author contributions: CS and MO collected specimens, MO compiled species list and described new species, CS and MO wrote manuscript.

Legal note: Sampling of bees and wasps for this study in Belize was conducted under a mission for Civil Service Switzerland and is therefore not allowed to be considered as part of the dissertation.

Abstract

Eighteen species of Dryinidae and one species of Sclerogibbidae are listed from Belize. Two new species of Dryinidae, *Anteon dykeae* Olmi, sp. nov. and *Dryinus schueepi* Olmi, sp. nov., are described from Belize, Corozal District. Keys to Neotropical species of *Anteon* and *Dryinus* are modified and include new species. Nine species of Dryinidae and one species of Sclerogibbidae are newly recorded from Belize. New records of Dryinidae are: four species from Panama, two species from Paraguay, and one species from Colombia, Mexico, Honduras, Venezuela, Ecuador, Bolivia and French Guiana. The dryinid and sclerogibbid fauna of Belize is still under-sampled and insufficiently known.

Key words

Drynidae, Sclerogibbidae, Belize, new species, new records, *Anteon dykeae*, *Dryinus schueepi*

Introduction

Belize is a small country of Central America, situated between Mexico, Guatemala, and the Caribbean Sea. Dryinidae and Sclerogibbidae (Hymenoptera: Chrysidoidea) are parasitoids respectively of Hemiptera Auchenorrhyncha (Guglielmino and Olmi 2007) and Embiidina (Olmi 2005). In the monograph of world Dryinidae published by Olmi (1984) two species were reported for the first time from Belize. At last, Olmi et al. (2000) recorded eight species in Belize. In the monograph of world Sclerogibbidae by Olmi (2005) no species were listed in Belize. In 2011 the study of new material collected by one of the authors (Schüep) has resulted in the discovery of two new species described herein, in addition to other species never quoted in Belize. These records provided the opportunity to compose a checklist of dryinids and sclerogibbids known from Belize.

Material and methods

Species descriptions follow the terminology used by Olmi (1984, 1999). The measurements reported are relative, except for the total length (head to metasomal tip, without the antennae), which is expressed in mm. In the descriptions POL is the distance between the inner edges of the two lateral ocelli; OL —between the inner edges of a lateral ocellus and the median ocellus; OOL is the distance from the outer edge of a lateral ocellus to the compound eye; OPL — from the posterior edge of a lateral ocellus to the occipital carina; TL — from the posterior edge of the eye to the occipital carina. The most part of the material studied in the present paper was collected in 2009 and 2010 with ground Malaise traps (B & S Entomological Services, UK) and yellow pan traps by one of the authors (Schüep).

The material studied in this paper is deposited in the following collections: Natural History Museum, Bern, Switzerland (BER); The Natural History Museum, London, United Kingdom; Canadian National Collection of Insects, Ottawa, Canada; Department of Entomology, University of California, Riverside, California, USA; Department of Entomology, Texas A. & M. University, Texas, USA; Faculté des Sciences Agronomiques de l'État, Gembloux, Belgium; Instituto Alexander von Humboldt, Santafé de Bogota, Colombia; Museo de Invertebratos G.B. Fairchild, Facultad de Ciencias Naturales y Exactas, Universidad de Panamá, Panamá; Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay; Natural History Museum, University of Kansas, Lawrence, USA; Natural History Museum of Los Angeles County, Los Angeles, USA; Department of Plant Protection, University of Tuscia, Viterbo, Italy (Massimo Olmi's collection); Provincial Museum of Alberta, Edmonton, Alberta, Canada; National Museum of Natural History, Washington, DC, USA.

Checklist of Dryinidae and Sclerogibbidae of Belize

Species with asterisk (*) are new country records for Belize.

Family Dryinidae

Subfamily Aphelopinae

Genus *Aphelopus* Dalman 1823

1. *Aphelopus diffusus* Olmi 1984
2. *Aphelopus trinitatis* Olmi 1984*

Subfamily Anteoninae

Genus *Deinodryinus* Perkins 1907

3. *Deinodryinus costaricanus* Olmi 1987a*
4. *Deinodryinus gauldi* Olmi 1991*
5. *Deinodryinus sublatifrons* Olmi 1999b*
6. *Deinodryinus trinidad* Olmi 1984*

Genus *Anteon* Jurine 1807

7. *Anteon albitarse* (Cameron 1888)*
8. *Anteon dykeae* Olmi, sp. nov.* (Fig. 1)
9. *Anteon panamense* Olmi 1984
10. *Anteon pilicorne* Ogloblin 1938*

Subfamily Dryininae

Genus *Dryinus* Latreille, 1804

11. *Dryinus argentinus* Olmi 1984*
12. *Dryinus belizensis* Olmi 1984
13. *Dryinus gibbosus* (Olmi 1984)*
14. *Dryinus schueepi* Olmi, sp. nov.* (Figs 2 and 3)
15. *Dryinus snellingi* Olmi 1986
16. *Dryinus wellingensis* Olmi 1984

Subfamily Gonatopodinae

Genus *Gonatopus* Ljungh 1810

17. *Gonatopus bartletti* Olmi 1984
18. *Gonatopus maidicolus* (Olmi 1987b)

Family Sclerogibbidae

Genus *Probethylus* Ashmead 1902

1. *Probethylus callani* Richards, 1939*

Description of new species

Anteon dykeae Olmi, sp. nov. (Fig. 1)

Etymology: This species is named after Miss Katie Dyke.

Types: Holotype, male, BELIZE: Corozal District, Sarteneja, La Isla Road Cenote, Low semi-deciduous forest, 18°20.115'N 88°7.713'W, 2 m a.s.l., 11-17.xii.2009, Malaise trap 1, C. Schüepp coll. (BER).

Diagnosis: Male with scutum mostly granulated; posterior surface of propodeum not sculptured by two longitudinal keels; distal apex of paramere broadly hollowed out (Fig. 1).

Description: Male: fully winged; length 2.7 mm. Head black, except mandible testaceous; antenna brown, except segment 1 testaceous; mesosoma black; metasoma brown; legs testaceous, except clubs of profemora partly brown, mesotibiae partly brown, metacoxae, clubs of metafemora and metatibiae partly black. Antenna hairy, filiform, with segment 3 triangular; antennal segments in following proportions: 10:6:6:5:5:5:5:5:6:8. Head dull, granulated and reticulate rugose; frontal line complete; face with two lateral keels around orbits directed towards antennal toruli; vertex with two hardly visible oblique keels connecting posterior ocelli to occipital carina; occipital carina complete; POL = 9; OL = 5; OOL = 6; OPL = 5; TL = 4; greatest breadth of posterior ocelli about as long as TL. Scutum dull, granulated, except anterior margin rugose. Notauli incomplete, reaching about 0.25 length of scutum. Scutellum and metanotum shiny, smooth, punctate, without sculpture among punctures. Propodeum reticulate rugose, with strong transverse keel between dorsal and posterior surface; posterior surface without longitudinal keels. Fore wing hyaline, without dark transverse bands; distal part of stigmal vein shorter than proximal part (2:8). Paramere with distal apex broadly hollowed out, without distal inner pointed process (Fig. 1). Tibial spurs 1/1/2. Female: unknown.

Distribution: Only known in the type locality.

Hosts: Unknown.

Comments: Because of the posterior surface of propodeum not sculptured by two longitudinal keels and the scutum mostly granulated, the male of *A. dykeae* is similar to those of *A. albitarse* (Cameron 1888), *A. mayanum* Olmi 1991, *A. desantisi* Virla 1998, *A. feralis* Olmi 1993, and *A. pilicornis* Ogloblin 1938.

Dryinus schueepi Olmi, sp. nov. (Figs 2 and 3)

Etymology: This species is named after the collector, Christof Schüepp.

Types: Holotype, female, BELIZE: Corozal District, Sarteneja, Mesatonich Road, Farmland/Agroforestry, 18°19.847'N 88°8.776'W, 3 m a.s.l., 22-28.i.2010, Malaise trap 3, C. Schüepp coll. (BER).

Diagnosis: Head rugose, unusually excavated; eye very bulging; POL shorter than greatest breadth of each posterior ocellus; OL about eleven times as long as POL; prothorax black, except lateral and

posterior margin of pronotum, including posterior tubercles, testaceous; fore wing with three dark transverse bands; propodeum without strong transverse keel between dorsal and posterior surface.

Description: Female (Fig. 3): fully winged; length 7.6 mm. Head black, except mandible, clypeus, part of gena and anterior margin of face between and around antennal toruli testaceous; palpus brown; antenna testaceous, except segments 4-5 and distal extremity of 3 brown; rest of segment 3 whitish; mesosoma black, except lateral and posterior margin of pronotum testaceous; pronotal tubercle testaceous; metasoma brown-testaceous; proleg brown, except tarsus, stalk of femur and part of tibia testaceous; mesoleg and metaleg brown, except metatrochanter testaceous. Antenna clavate; antennal segments in following proportions: 19:7:41:19:15:12:9:8:7:10; rhinaria present in antennal segments 5–10. Head hairy, dull, rugose, very excavated, with eye very bulging; frontal line complete; occipital carina absent; temple absent; POL = 1; OL = 11; OOL = 10; POL much shorter than greatest breadth of posterior ocelli (1:3.5). Pronotum dull, hairy, sculptured by fine striae situated around disc, crossed by weak anterior transverse impression; pronotal tubercle not reaching fore-tegula. Scutum and scutellum dull, reticulate rugose. Notauli absent. Metanotum shiny, hairy, punctate, without sculpture among punctures. Propodeum completely reticulate rugose, without transverse keel between dorsal and posterior surface; dorsal surface with some longitudinal keels connected by short transverse keels or areolae; posterior surface with two longitudinal keels and median area dull, rugose. Mesopleuron and metapleuron densely hairy, reticulate rugose. Fore wing with three dark transverse bands; distal part of stigmal vein longer than proximal part (20:14). Fore tarsal segments in following proportions: 21:4:10:21:40. Enlarged claw not spatulate (Fig. 2), with large subdistal tooth and one row of 15 lamellae and 1 bristle. Segment 5 of fore tarsus (Fig. 2) with two rows of approximately 35 lamellae; distal apex with at least 30 lamellae. Tibial spurs 1, 1, 2. Male: unknown.

Distribution. Only known in the type locality.

Hosts: Unknown.

Comments: According to the systematics of the Neotropical *Dryinus* proposed by Olmi (1993b), *D. schueepi* belongs to *ruficauda* group. Because of the head rugose and unusually excavated, the eye very bulging and POL shorter than greatest breadth of each posterior ocellus, the female of *D. schueepi* is similar to that of *D. putus* Olmi 1998. The main differences between these two species are the following:

Dryinus putus (Olmi): Prothorax testaceous-reddish; fore wing with two dark transverse bands; propodeum with strong transverse keel between dorsal and posterior surface; head with OL about three times as long as POL.

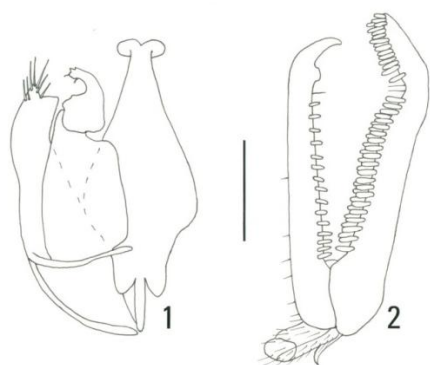
Dryinus schueepi Olmi sp. nov: Prothorax black, except lateral and posterior margin of pronotum, including posterior tubercles testaceous; fore wing with three dark transverse bands; propodeum without strong transverse keel between dorsal and posterior surface; head with OL about eleven times as long as POL.

Discussion

The checklist of Dryinidae and Sclerogibbidae of Belize presented in this paper includes one species of sclerogibbids and 18 species of dryinids, of which two new species, *Anteon dykeae* sp. nov. and *Dryinus schueepi* sp. nov., are described herein. The description of each new species is based on the study of one only specimen. The authors know that usually descriptions of new taxa should be based on more individuals. However, Dryinidae are so rare that it is not common to find more than one specimen of each species. In addition, on the basis of the experience and knowledge of one of the authors (Olmi), the two species are sufficiently characterized to justify their descriptions.

Thirteen (72%) of the 18 Belizean species of Dryinidae have a large geographic distribution in the Neotropics, in one case (*Anteon albitarse* (Cameron)) with an extension to the USA. One species (*Deinodryinus sublatifrons* Olmi) is recorded outside of Belize only from Costa Rica; *Dryinus belizensis* Olmi is known only from Mexico. Apparently, three species (16%) are endemic in Belize. In two districts (Belize and Orange Walk) no species are known. In Corozal, thanks to the research of one of the authors (Schüepf), ten species are known. In the other districts the number of known species is very low: Cayo: two species; Stann Creek: four species; Toledo: two species. A comparison with other Neotropical countries where the dryinid fauna is best known indicates the research status on Dryinidae in Belize. In Costa Rica 148 species are recorded (Olmi 1993a, Olmi et al. 2000); in Brazil 147 species (Coelho et al. 2011, Olmi 2011); Argentina 130 species (Virla and Olmi 2008); in Venezuela 73 species (Olmi et al. 2000); in Mexico 135 species (Moya Raygoza and Olmi 2010). Belize can probably be best compared with Costa Rica due to the geographical proximity, the similar comparable size (Costa Rica 51100 km², Belize 22966 km²), and the high diversity of habitat types in both countries (e.g. dry, semi-deciduous forest, tropical wet forest, tropical montane forest, mangrove and littoral forest). From this comparison (Costa Rica 148 species, Belize 18 species) we conclude that the dryinid fauna of Belize is under-sampled and therefore insufficiently known. However, in both countries, the biology of dryinids (including their hosts) is almost unknown, resulting in large difficulties to compare the two faunas on the basis of ecological criteria. These difficulties arise from the collection methods used so far: instead of rearing dryinids directly from hosts, they were sampled mainly by Malaise and yellow pan traps. Dryinidae are important natural enemies of leafhoppers pests on cultivated plants. Some of them are currently used in biological control programmes in several countries (Olmi 2000).

The Sclerogibbidae require more research in Belize. The second and common Neotropical species of *Probethylus*, *P. schwarzi* Ashmead 1902, is probably present in that country. This species is known from all nearest countries: Mexico, Guatemala and Costa Rica (Olmi 2005).

Figures

Figures 1 and 2. 1. *Anteon dykeae* sp. nov., male, holotype, genitalia (right half removed), scale bar = 0.12 mm; 2. *Dryinus schueeppi* sp. nov., female, holotype, chela, scale bar = 0.31 mm.



Figure 3. *Dryinus schueeppi* sp. nov., female, holotype. Length 7.6 mm

Chapter 3: Pollination

Disentangling multiple drivers of pollination in a landscape-scale experiment

Information

This chapter was submitted on 27 March 2013 as:

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Author contributions: CS, FH and MHE designed experiment, CS performed experiment, CS and MHE analysed data and wrote manuscript.

Abstract

Pollination is essential for the reproductive success of many wild and crop plants. Loss and isolation of (semi-) natural habitats in agricultural landscapes are among the main drivers causing pollinator declines and endangering pollination services. We investigated the independent effects of these drivers on pollination of young cherry trees in a landscape-scale experiment. We included (1) isolation of study trees from other cherry trees, (2) the amount of cherry trees in the landscape, (3) the isolation and (4) amount of woody habitats providing nesting and floral resources for pollinators. At the local scale, we considered effects of (5) cherry flower density and (6) heterospecific flower availability. Fruit set on cherry trees was pollen-limited. Pollinators visited flowers more often in landscapes with high amount of woody habitat and at sites with lower isolation from the next cherry tree. In contrast, fruit set was not determined by the amount of woody habitat in the landscape but was reduced by isolation from the next cherry tree and by a high local density of heterospecific flowers. Thus, pollination depended more on the proximity of suitable pollen sources and competition from co-flowering species than on factors enhancing pollinating insects. It proved important to differentiate between the plant and pollinator perspective, as well as between habitat amount and isolation to understand the delivery of an agriculturally important ecosystem service.

Key words

Fragmentation per se, composition versus configuration, beneficial densities versus ecosystem service, Apiformes, bees, Empididae, Syrphidae, dilution and concentration effects

Introduction

IMPORTANCE OF POLLINATION

Effective animal pollination is an extremely important ecosystem service. It directly benefits humans through higher fruit set and crop yield (Klein et al. 2007, Garibaldi et al. 2013, Tylianakis 2013). Already today, 75% of crop species and 35% of crop production worldwide depend at least partly on animal pollination (Klein et al. 2007). The increasing dependence of agriculture on animal-pollinated crops (Aizen et al. 2008) raises the expectation that pollination shortage (Potts et al. 2010) will become a global concern in near future (Garibaldi et al. 2011a, Tylianakis 2013). Pollinator-mediated sexual reproduction supports global plant biodiversity through increased fecundity and gene flow (Groom 1998, Aguilar et al. 2006). Through sexual reproduction, plants benefit from pollen and seed dispersal, the opportunity to increase or maintain genetic diversity and therefore the potential to adapt to new environments (Cunningham 2000, Wilcock and Neiland 2002).

HABITAT LOSS VERSUS FRAGMENTATION

Expansion of agricultural land use leads to loss and fragmentation of (semi-) natural habitats, two key factors threatening biodiversity and ecosystem services such as pollination (Tscharntke et al. 2005, Winfree et al. 2009). The effects of fragmentation on pollination are especially strong in self-incompatible plants where the presence of conspecific plants as pollen donors within foraging distance of pollinators is essential for reproductive success (Aguilar et al. 2006). Historically, habitat loss and fragmentation effects were mostly measured at the local, not the landscape scale, and fragmentation *per se* was rarely separated from habitat loss (Fahrig 2003, Lindenmayer and Fischer 2007, Potts et al. 2010, Hadley and Betts 2012, Tscharntke et al. 2012). Knowledge on the independent effects of habitat loss and fragmentation is necessary for an effective landscape management for biodiversity and ecosystem services (Hadley and Betts 2012) and it remains an important research issue how (semi-) natural habitats should best be configured to optimise ecosystem services (Kremen 2005, Kremen et al. 2007). The amount of suitable habitat determines the pool of available species and individuals in a given landscape whereas habitat isolation (as a measure of fragmentation) constrains access from this species pool (Tscharntke et al. 2012). This access might be especially important in landscapes with low amount of suitable habitat where local biodiversity is primarily determined by landscape wide remnant communities compared to rich landscape where species pool is high everywhere (Andren 1994, Tscharntke et al. 2005, Tscharntke et al. 2012). Habitat isolation affects species negatively by forcing them to exploit several disconnected resources for foraging or nesting (Isaacs et al. 2009, Tscharntke et al. 2012). Further, isolated habitats may lie outside of the perception range or be avoided because of higher predation risk in the matrix (Hadley and Betts 2012).

PLANT POPULATION, POLLINATOR HABITAT, AND POLLINATOR MOVEMENT

Small or isolated plant populations may suffer decreased reproduction due to lowered pollen quantity and/or quality relative to non-isolated populations (Kremen et al. 2007). This effect of habitat isolation on pollination can be mediated through lower access to pollen donors (i.e. isolation of the plant population), through lowered pollinator density (caused by isolation of pollinator habitat), and through changes in pollinator movement (Hadley and Betts 2012). Isolated plant populations can show lower pollination success independent of pollinator visitation because of a lack of compatible donor plants (Duncan et al. 2004). In turn, the absence of pollinators can decrease pollination success even in situations where the availability of donor plants is high (Kremen et al. 2007). Therefore, both habitat requirements of pollinators (pollinator perspective) and the spatial distribution of plant populations (plant perspective) have to be taken into account. Finally, visitation of pollinators and fruit set can be affected by pollinator movement (Hadley and Betts 2012): Local flower availability may positively affect visitation and fruit set by attracting more pollinators from the landscape pool (concentration effect), or may negatively affect visitation and fruit set by increasing intra- or interspecific competition for pollinators (dilution effect), resulting in lower visitation per flower at sites with more flowers (Veddeler et al. 2006, Kremen et al. 2007, Jha and Vandermeer 2009, Tschamtker et al. 2012). Furthermore, direct negative effects of local heterospecific flower resources on fruit set can arise independent of visitation because of lower quality of pollen mix transported by pollinators (mix with less conspecific pollen) (Kremen et al. 2007). In this study, we tested the effects of plant population amount and isolation, pollinator habitat amount and isolation, and local (con- and heterospecific) flower availability on pollinator visitation and fruit set using young cherry trees, a self-incompatible crop plant (Schueler et al. 2006).

WOODY HABITAT FOR POLLINATORS

Many organisms of temperate agricultural landscapes depend on woody structures because of rich food resources, provision of nesting sites and low disturbance (Duelli and Obrist 2003, Kremen et al. 2004, Holzschuh et al. 2009, Sanderson et al. 2009). Therefore, biodiversity and ecosystem services are strongly influenced by woody habitats (Herzog 1998, Kremen et al. 2004, Klein et al. 2007, Farwig et al. 2009, Schüepp et al. 2011, Watson et al. 2011, Diekötter and Crist 2013). Although pollinators also use floral resources and nesting sites of open (non-woody) habitats, the importance of woody habitats for pollinators may be especially strong in spring, when most of the extensive blooms (except *Taraxacum*) belong to trees or shrubs (*Prunus avium*, *P. spinosa*) and understory herbs are in bloom (Taki et al. 2007, Watson et al. 2011), and because sunny (due to missing canopy foliage) and relatively undisturbed ground provides optimal nesting sites for ground nesting bees (Westrich 1989, Herrmann 2000). Cavity nesting bees also depend on woody habitats to find nesting sites in dead wood (Westrich 1989). Here, we mainly focus on the analysis of woody habitats as suitable habitats

for pollinators but we also statistically control for possible effects of open (non-woody) semi-natural habitats on pollination.

HYPOTHESES

We used a landscape-scale experiment with systematically planted young cherry trees, as an insect-pollinated model plant, to test the following predictions for pollination services in fragmented agricultural landscapes (Fig. 1).

1. Visitation of pollinators and pollination success (fruit set) are higher in landscapes with high amount of woody habitat and low isolation to the next woody habitat. Woody habitats were considered as main habitats providing nesting and floral resources for pollinators in our landscapes in spring (pollinator habitat).
2. Effects of isolation from woody habitat are stronger in landscapes with low amount of woody habitats than in landscapes with high amounts (interacting effects between isolation and amount of woody habitat).
3. Visitation and pollination success are influenced by the spatial distribution of cherry trees (plant population) in the landscape. Visitation and pollination success increase in landscapes with higher amount of cherry trees and in study sites less isolated from conspecifics because of better outcross pollen availability.
4. Heterospecific flower resources, both on the ground and in shrubs, as well as conspecific flower availability affect pollinator visitation and pollination success.

Materials and methods

EXPERIMENTAL DESIGN AND LANDSCAPE VARIABLES

The study was conducted in 2011 in the Swiss plateau between the cities of Bern, Solothurn, and Fribourg, where agricultural areas are interspersed with forest. We used 30 spatially separated landscape sectors distributed over an area of 23 by 32 km and varying in altitude between 465 and 705 m above sea level. Experimental sites in the centre of each landscape sector consisted of an 18-m-long rows of seven 7-year-old wild cherry trees (*Prunus avium* L.) on permanent grassland. We planted cherry trees in 2008 for the experiment and managed them since then in a standardised manner (see Farwig et al. 2009, Schüepp et al. 2011). All 210 trees came from the same tree nursery and were of similar size and genotype. The sites were selected systematically to cover a gradient in the percentage of woody habitat in a 500 m buffer and to differ in their level of local isolation from woody habitat. We chose the landscape scale of 500 m buffer because solitary bees as main pollinators of young cherry trees (see Results) are influenced by spatial scales of a few hundred meters (Gathmann and Tschardt 2002, Steffan-Dewenter et al. 2002, Zurbuchen et al. 2010). Woody habitats comprised hedgerows, orchards, single-standing trees, treelines, and forest. The percentage of these habitat types

in a 500-m buffer around the sites varied from 4 to 74%. Isolation had three levels: ten sites were located at the edge of dense and tall-growing forest representing no isolation from woody habitat. The remaining 20 sites were located in a distance of 100 - 200 m from the next forest, half of them connected by small-sized woody habitats such as hedgerows or trees ('connected') and the other half isolated from any woody habitat by 100 - 200 m ('isolated'). Location and type of woody habitats were derived from national digital land-use maps (vector25, swisstopo, Wabern) and verified using aerial photographs and field inspection. Sites with different levels of isolation and with different percentages of woody habitat in the surrounding landscape were spatially interspersed ($p > 0.19$ for relationships of x and y coordinates with isolation and percentage of woody habitat, respectively) (Schüepp et al. 2011). Because of little tree growth and low flowering densities we omitted 2 sites from the analysis of fruit set and 3 sites for the analysis of flower visitation. To assess isolation and amount of target plant populations, we measured the distance of each study site to the next wild or cultivated cherry tree taller than 3 m (cherry isolation) and the number of wild or cultivated cherry trees within each landscape sector (cherry amount) with field inspections. To test possible effects of open (non-woody) semi-natural habitats on pollinators and cherry fruit set, we assessed the percentage of low-intensity grasslands and sown wildflower strips per landscape using official records of ecological compensation areas (GEOPORTAL, Kanton Bern) and field inspections. We did not test the effect of cross-habitat spillover of pollinators from oilseed rape fields into cherry trees because oilseed rape started to bloom only at the very end of the cherry flowering period and was therefore expected not to have any effect on cherry pollination.

LOCAL VARIABLES

Local conspecific flower density was estimated counting the fully open cherry flowers (stigma and anthers visible) on all seven cherry trees per site (no. of cherry flowers). Local heterospecific flower availability was estimated counting the number of flowering shrubs (mostly *Prunus spinosa*) within 50 m buffer around the focal cherry tree line (no. of shrubs) and counting the number of flowers or inflorescences (in Apiaceae and Asteraceae) on the ground in four 1 m² plots per site (ground flower cover). The four plots had a standardised position within the 20 * 2 m grassland strip below the cherry trees. All local variables were measured three times during the flowering period and averaged per site for analysis.

FLOWER VISITATION

We used high-definition handycams (Sony HDR-CX115E/B) to assess flower visitors on cherry trees. At each site, we filmed a group of 2-3 flowers (rarely 1 or 4, mean=2.37, sd=0.75) for 30 min on three different days during the bloom, resulting in recordings of approx. 225 flower-minutes per site. Each of the three films per site was recorded at a different daytime (between 10-12, 12-14, and 14-16). During each video, maximal wind speed (m/s) was assessed by measuring wind speed three times for

two minutes (start, middle, and end of video) with hand anemometers (PCE-A 420, PCE Deutschland GmbH). Maximal wind speed was assessed for each video and then averaged per site for analysis. As the number of flowers filmed slightly differed between sites, we calculated the mean number of flowers filmed per site (flower per video) to control for in our analysis (included as variable in full models). Based on videos, we derived the number of insect visitors to flowers (visitation rate), the species richness of visitors, the mean duration per insect visit (duration), and the behaviour of the visitor on the flower. According to the behaviour of the visitor, each visit was assigned to one of three categories: Visits touching stigma and anthers (score 3), only anthers (score 2) or only petals (score 1). Because flower visitors vary in their effectiveness (Kremen 2005, Kremen et al. 2007) we separated visitor groups that are potential pollinators, i.e. consistently touched stigma and anthers, from those only rarely and hazardously touching stigma or anthers. We only used potential pollinator groups (with a mean visit score ≥ 2.5) in analysis of flower visitation (Table S1). With the help of a specialist (see Acknowledgments) and a reference collection, all bee visitors were determined to species level. Other flower visitors were determined to family or superfamily level. Visitation data derived from three videos per site were pooled for analysis.

FRUIT SET

At half of the sites (N=15) sixteen groups of flower buds located all over the canopy were marked on four different trees per site and randomly assigned to four treatments: open pollination ('open'), bagged flowers ('control'), self-pollination by hand ('self'), or cross-pollination by hand ('cross'). At the remaining sites, only eight groups were marked and randomly assigned to 'open' and 'control' treatments. Treatments were applied approximately one week before bloom. In treatment 'open', groups were freely exposed to pollinators. In treatment 'control', 'self' and 'cross', flower groups were bagged with polyethylene bags (mesh size 0.4 mm; Sefar AG, Switzerland) to prevent access of pollinating insects, but permitting access of pollen transported by wind (Dafni and Dafni 1992). During the bloom, in treatment 'self' all flowers were hand pollinated by paintbrush 2-3 times (on different days) with pollen obtained from unmarked flowers of the same tree. In treatment 'cross' marked flowers were cross-pollinated with pollen obtained from at least 3 different wild cherry trees from forest edges in our study area. Branches of these trees were brought to the lab, stored in cold chambers, and then kept at room temperature until 3 days before pollen was used for hand-pollination. We obtained pollen by twisting cherry flowers within small containers the evening before pollen was used in the field. The 'control' treatment did not receive any additional handlings apart of being bagged. Immediately after the bloom (petal abscission), all bags were removed to avoid climatic impacts on developing fruits. We had to exclude 42 of the 344 marked groups from our analysis because of broken twigs, herbivores eating flowers, and buds not developing into fertile flowers. Fruit set (pollination success) per treatment was calculated as the percentage of intact marked flowers (not damaged by herbivores) that developed into swollen green fruits approx. 3 weeks after pollination per

site. This measure has shown to be highly correlated with the final fruit set in cherry trees (Holzschuh et al. 2012).

STATISTICAL ANALYSES

All analyses were performed in the open source software R 2.15.0 (R Development Core Team 2012) using the packages lme4 (Bates et al. 2012), and MuMIn (Barton 2012). We performed a generalised linear mixed effects model (GLMER) with binomial error distribution to assess the effects of pollination treatments (fixed effect) on fruit set. Marked flowers nested within trees and trees nested within sites were included as random effects. Inference was based on model comparison (ANOVA). Pairwise differences between treatment on z-values from GLMER model summary. To test the effect of visitation rate (square root-transformed to obtain homoscedasticity) on fruit set of the ‘open’ pollination treatment, we used a generalised linear model (GLM) with quasi-binomial error distribution. To test the effects of landscape and local variables on visitation rate, duration per visit, and fruit set of ‘open’ and ‘control’ treatments (all variables pooled per site) we performed GLM with poisson error distribution for visitation (count data) and GLM with binomial error distribution for fruit set (proportion data). Flower visitor species richness was not used in the models because it was highly positively correlated with visitation rate (Pearson’s correlation, $r=0.84$, $n=25$, $p<0.001$). We used quasi-distributions if dispersion parameter was > 1.5 (overdispersion) and removed outlier with a Cook’s distance > 1 . In all three tests involving landscapes and local variables, best models were selected from full models with automated model selection using dredge function (Barton 2012) based on Akaike’s Information Criterion for small samples sizes (AICc, or QAICc in case of overdispersion). For full models, see Tables S3 and S4. Some explanatory variables were significantly correlated with each other (Table S2). If a variable (x_1) included in the final model was correlated with any other variable (x_2) not contained in the final model, we report delta-(Q)AICc values between the final model and the best model in which x_2 appears in place of x_1 (hereafter referred as alternative model). We accepted the final model if delta-(Q)AICc of the alternative model was > 3 (Tables S3 and S4).

Results

FLOWER VISITATION

In total, 127 insect visits to cherry flowers were filmed (Hymenoptera: 54, Diptera: 51, Coleoptera: 21, Heteroptera 1). Honey bees were only observed at one site. Bees (Apiformes) and two families of flies (Empididae, Syrphidae) showed a mean visit behaviour score ≥ 2.5 and were therefore considered as potential pollinators and used for modelling flower visitation. Wild bee visitors comprised *Andrena haemorrhoa*, *Andrena cf. gravida*, *Andrena nitida*, and *Osmia bicornis* (Table S1). Visitation rate was best explained by cherry isolation and wood amount: visitation rate increased with decreasing isolation from the next cherry tree ($z=-3.58$, $df=24$, $p<0.001$) and with increasing amount of woody habitat in

the landscape ($z=3.15$, $df=24$, $p=0.002$) (Figs 1 and 2). Cherry isolation and woody habitat amount explained together 35% of the total model deviance. Excluding the few visits by honey bees did not change the variables retained in the best model. Duration per visit was only explained by wind: higher wind speed was associated with increased visitation time ($t=2.53$, $df=25$, $p=0.024$, explained deviance by wind: 26%).

FRUIT SET

In total, 203 groups of flowers were included in our experiment ('control': 69, 'cross': 31, 'open': 72, and 'self': 31). Fruit set was strongly affected by the different pollination treatments (Fig. 3A): 52% of 'cross' flowers, 34% of 'open' flowers, 5% of 'control' flowers, and 4% of 'self' flowers set fruit (GLMER: 266 observations, groups: 77 trees at 28 sites, $\chi^2=178$, $p<0.001$). 'Control' and 'self' treatments had a significantly lower fruit set than 'open' and 'bagged' treatments ($z>7.95$, $p<0.001$). 'Cross' treatment had a significantly higher fruit set than 'open' flowers ($z=2.99$, $p=0.003$). 'Control' and 'self' treatments did not differ ($z=0.24$, $p=0.8$). Fruit set of 'open' flowers was significantly related to visitation rate ($t=2.13$, $df=25$, $p=0.043$) (Figs 1 and 3B).

When testing effects of landscape and local variables on fruit set of 'open' flowers, fruit set was best explained by two variables: it increased with decreasing isolation from the next cherry tree ($t=-3.27$, $df=25$, $p=0.003$) and decreased with increasing numbers of heterospecific shrubs in bloom within a 50 m buffer around studied trees ($t=2.67$, $df=25$, $p=0.013$) (Figs 1 and 4). Cherry isolation and no. of shrubs explained 37% of the total model deviance. Fruit set of 'control' flowers was best explained by wind, cherry isolation and isolation from woody habitat but wind was the only significant variable increasing fruit set of 'control' flowers ($t=2.23$, $df=22$, $p=0.037$). Wind, cherry isolation and isolation from woody habitat explained 45% of the total model deviance.

Discussion

We show how landscape management can affect the delivery of pollination services (Fig. 1). The amount of pollinator habitat in the landscape, but not isolation from these habitats, increased the number of visits to cherry flowers. Isolation of studied cherry trees from conspecifics decreased visitation rates and fruit set. Therefore, visitation rate was correlated with pollination success. At the local scale, heterospecific flowers decreased pollination success but not visitation rates.

POLLINATOR HABITAT AMOUNT

The amount of suitable habitats in the landscape determines the pool of available species and individuals and increases the chance of local populations to persist (Tscharntke et al. 2012). In accordance with this prediction (hypothesis 1), we found higher visitation rates in landscapes with higher amount of woody habitats (Fig. 1B). In contrast to the frequent expectation that flower-rich open (non-woody) semi-natural habitats favour pollinator communities (Albrecht et al. 2007),

visitation rates did not increase with higher amount of open semi-natural habitats. In our study landscapes, open semi-natural habitats were relatively rare (below 8%, except one site with 12%). A minimal threshold of 20% of semi-natural habitats was suggested to ensure meaningful protection of biodiversity and ecosystem services (Tscharntke et al. 2012). Thus, open semi-natural habitats may have been too rare in the studied landscapes to have a strong effect on pollinator activity. In contrast, woody habitats covered more than 20% of the area in 15 out of 30 studied landscapes. In spring, woody habitats including forests provide good conditions for ground nesting bees (most wild bee species observed on cherry flowers; Table S1) because of a combination of relatively undisturbed and sunny ground due to missing canopy foliage (Westrich 1989, Herrmann 2000). Pollinators nesting in the forests are known to enter open landscape for foraging trips (Herrmann 2000). Additionally, woody habitats provide abundant food resources in spring in the form of vernal blooms of trees, shrubs and ground flowering plants (Taki et al. 2007, Watson et al. 2011, Breitbach et al. 2012). The concentration of these resources in spring may explain why woody habitats were less important for bee communities sampled in the same landscapes but over the entire vegetation period (Schüepp et al. 2011). In contrast to a study in almonds (Klein et al. 2012), the positive effect of amount of suitable pollinator habitat on visitation did not translate into higher fruit set, showing that the availability of pollinators is not always limiting pollination success (Hadley and Betts 2012). The effectiveness of pollen transfer may rather depend on the availability of outcross pollen (see section ‘Spatial distribution of plant population’ below). This may be a reason why fruit set is generally decreasing less steeply with distance from semi-natural habitats than visitation (Ricketts et al. 2008, Garibaldi et al. 2011b).

POLLINATOR HABITAT ISOLATION

Isolation from woody habitats, as a measure of fragmentation *per se*, was not relevant for pollinators at the investigated scale (100 to 200 m), showing the importance of separating isolation and habitat amount (Fahrig 2003, Lindenmayer and Fischer 2007, Potts et al. 2010, Hadley and Betts 2012, Tscharntke et al. 2012). Mean visitation to flowers was estimated to decrease with isolation from semi-natural habitats by 27% at 1 km (Garibaldi et al. 2011b) or 50% at 600 m (Ricketts et al. 2008). Therefore, we cannot exclude the scale of isolation we used was at the lower limits to affect pollinator activity although it was chosen within the predicted mean foraging ranges of solitary bees (Gathmann and Tscharntke 2002, Steffan-Dewenter et al. 2002, Zurbuchen et al. 2010). The concept of mobile link compensation (discussed in Breitbach et al. (2012)) would predict that the absence of isolation effects is caused by pollinators compensating isolation with longer foraging distances. In this study, this remains speculative as we did not test foraging duration per site, a measure expected to increase in isolated populations because of higher movement costs (Kremen et al. 2007). Furthermore, pollinators may not perceive the open agricultural matrix as a resource depleted barrier (Wilcock and Neiland 2002). The absence of an interaction between habitat amount and isolation (hypothesis 2) gives no

support for the prediction that isolation becomes more important in simplified landscapes with lower amount of semi-natural habitats (Tscharntke et al. 2012).

SPATIAL DISTRIBUTION OF PLANT POPULATION

In accordance with our predictions (hypothesis 3), we found a strong reduction of pollination success with isolation from cherry trees (Fig. 4A). Further, we proved pollen limitation in our study system by showing a significantly higher fruit set when pollination was artificially maximized by supplementing compatible pollen by hand ('cross' treatment) compared to insect pollinated flowers ('open') (Fig. 3A). Pollen limitation in self-incompatible plants can be explained by reduced pollinator densities or by a lack of compatible pollen grains transported to stigma at isolated sites (Wilcock and Neiland 2002). Here, fruit set was correlated with visitation rate, suggesting that pollen limitation is, at least partially, happening because of reduced pollinator visitation. However, this effect is reinforced to an unknown degree by the lack of compatible pollen sources stimulating fruit set. Visitation rate and richness of visiting insects were highly correlated (Pearson's correlation, $r=0.84$, $n=25$, $p<0.001$). Thus, it remains unclear whether plant pollination success was increased by higher visitation rates or by diversity effects (Hoehn et al. 2008, Albrecht et al. 2012). Effects of isolation from the next conspecific plant on fruit set have been reported earlier (Groom 1998) and human disturbance is known to disrupt plant-pollinator interactions causing outcross pollen limitation (Ghazoul 2005, Eckert et al. 2010). As visitation rates declined with cherry tree isolation (Fig. 2A) we suspect flower consistency of wild pollinators to cherry. All bee visitors were flower generalists (polylectic) (Amiet 2010) but generalist pollinators may temporally switch strategy and become specialised in times of low flower availability (Hadley and Betts 2012). Alternatively, higher visitation at less isolated sites can be explained by a spill over from concentrated pollinator communities around cherry trees. Both visitation rates and fruit set dropped equally by approximately 75% along 350 m of cherry isolation (Figs 2A and 4A). Declines in visitation and fruit set are commonly not parallel (Ricketts et al. 2008, Garibaldi et al. 2011b) but may be observed if first, local plant populations are so small that compatible pollen has to come from outside the population or second, if isolation directly measures distance from nearest pollen donors. For example, isolation from woody habitat negatively affected fruit set of primroses (*Primula elatior*) in the same landscapes (Farwig et al. 2009) possibly because distance to forest not only reflected isolation from suitable habitat for pollinators but also from target plant populations. Surprisingly for an insect pollinated plant, isolation from the next cherry tree and wind explained fruit set of bagged 'control' flowers best. This indicates that wind plays a role in cherry pollination when suitable pollen donors are close. The amount of cherry trees in the landscape neither affected visitation nor pollination success.

LOCAL FLOWER DENSITIES

Because plant density can affect pollination at different spatial scales (Hadley and Betts 2012) we tested effects of target plant density not only at the landscape scale (cherry isolation and amount) but also at the local scale. In contrast to our predictions (hypothesis 4), we found no change in visitation or pollination success at sites with different densities of cherry flowers. Higher number of cherry flowers on study trees (local conspecific flower density) neither attracted pollinators from the landscape (concentration effect) nor diluted them (Veddeler et al. 2006, Tschardt et al. 2012). Furthermore, ground flowering plants seemed not to influence flower visitors on cherry trees, in agreement with findings from mature cherry trees in Germany (Holzschuh et al. 2012). Fruit set was negatively related to the number of heterospecific shrubs in bloom within a buffer of 50 m (Fig. 4B). This effect was not associated with decreasing visitation rates, contradicting the hypothesis of local dilution effects (Veddeler et al. 2006, Tschardt et al. 2012). Instead, it suggests that the pollen mix of visiting insects contains a higher share of heterospecific pollen at sites with high heterospecific pollen availability (Wilcock and Neiland 2002). The movement between con- and heterospecific flowers possibly led to the deposition of more heterospecific pollen on cherry stigmas causing pollen clogging (block of stamens) or chemical inhibition of pollen tube growth (Wilcock and Neiland 2002).

Conclusions

Our study demonstrates that landscape management can affect the delivery of an agriculturally important ecosystem service. The amount of woody habitat, but not isolation, increased insect visitation rates to cherry flowers. In contrast, the only landscape variable affecting fruit set was isolation of studied trees from conspecifics. These results reveal the importance of considering both the pollinator perspective and the plant perspective at the landscape scale. Further, it extends the understanding of independent effects of habitat isolation (as a measure of fragmentation) and habitat loss. At the local scale, competition from co-flowering species (measured as density of heterospecific flowers) decreased pollination success but not visitation, suggesting that movements of pollinators between different species reduce the quality of pollen mix transported. Overall, flower visiting pollinators and pollination success are affected differently, at multiple spatial scales, by landscape habitat loss, isolation of habitats and local flower resources. All of these aspects need to be considered to understand the pollination services provided by mobile organisms.

Figures

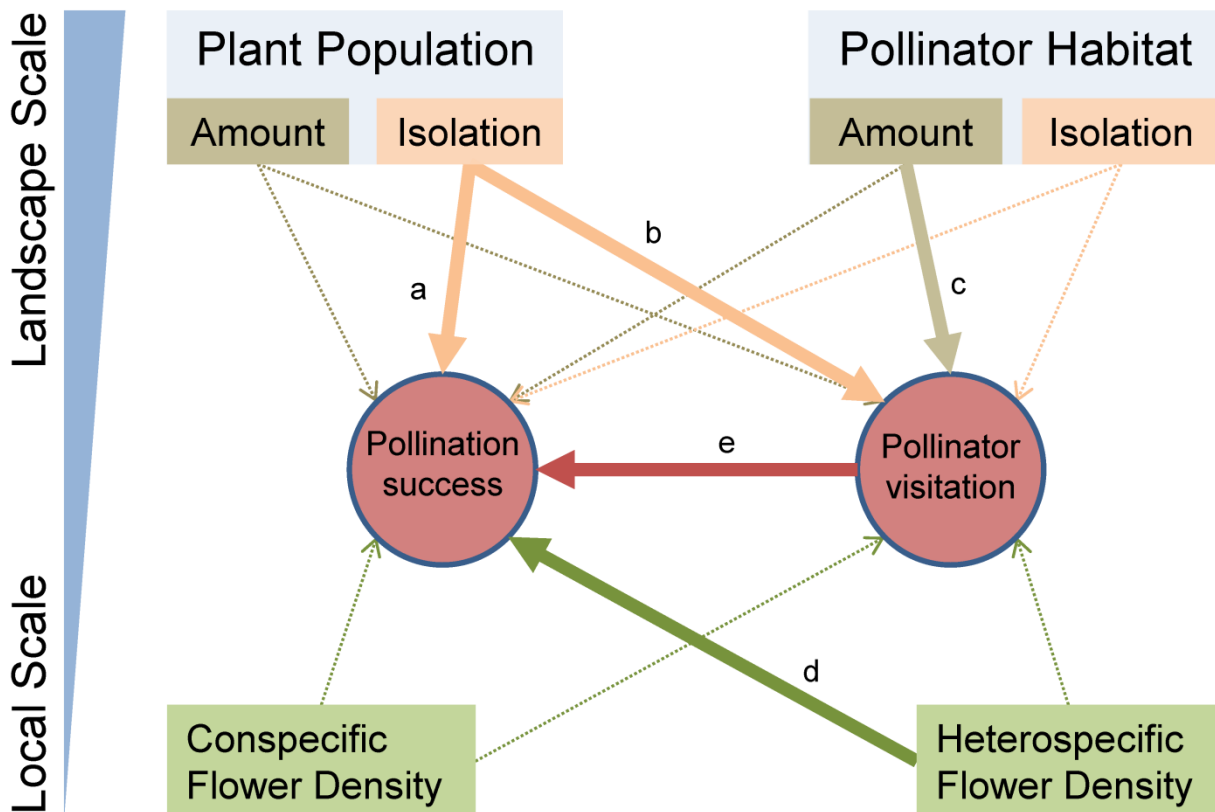


Figure 1. Disentangling key aspects of pollination in fragmented landscapes. Separation of the spatial distribution of target plant population *versus* pollinator habitat, habitat amount *versus* isolation (as a measure of fragmentation), local (50 m buffer) *versus* landscape scale (100-500 m buffer), and beneficial densities (pollinator visitation) *versus* provision of ecosystem service (pollination success). Dotted arrows show hypothesized impacts, bold arrows significant impacts derived from best models (see Results). Increased isolation of cherry trees, but not the amount of cherry trees in the landscape, was associated with (a) lower fruit set and (b) decreased number of flower visits. (c) High amount of woody habitats (pollinator habitat) at the landscape scale, but not isolation from these habitats, was associated with a high number of flower visits. Pollinator habitat amount did not impact pollination success directly. (d) Increased number of heterospecific shrubs in bloom on the local scale, but not the density of conspecific flowers, was directly associated with lower fruit set without changing rates of flower visitation. (e) Increased number of flower visits related to higher fruit set. Figure based on ideas from Hadley and Betts (2012).

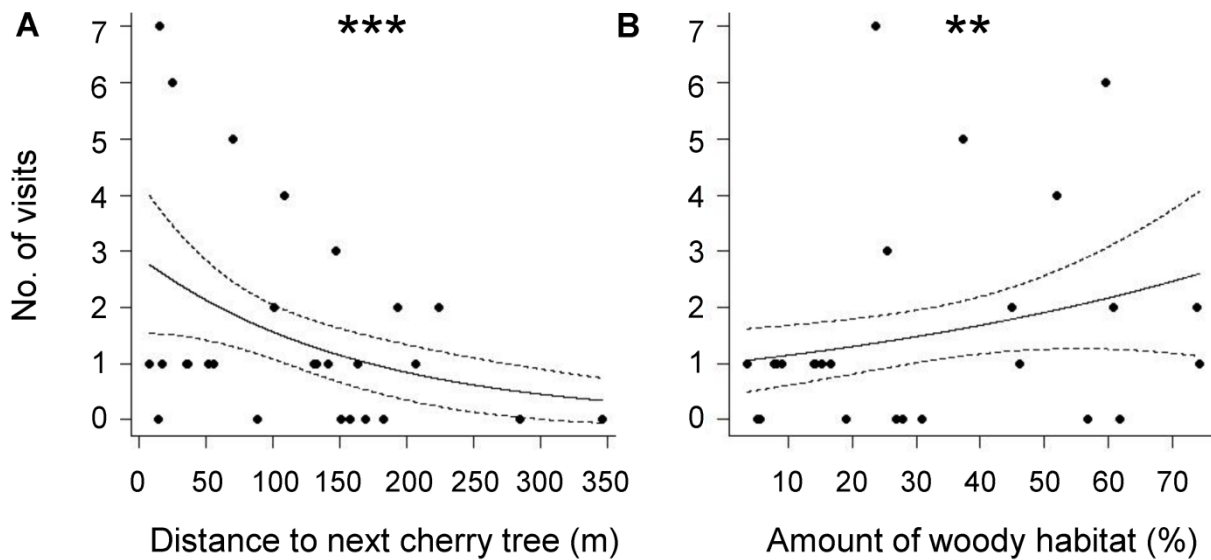


Figure 2. Pollinator visitation. Number of insect visits to flowers during 90 min of video observation in relation to (A) distance to next wild or cultivated cherry tree and (B) the amount of woody habitat in the landscape (500 m buffer around study site). Results based on best-fitting GLM (poisson error distribution) according to AICc model selection. Solid lines show predicted values of best-fitting model, dashed lines are estimated standard errors. Dispersion parameter = 1.3, residual df = 24, significance levels: *** p<0.001, ** p<0.01, explained deviance = 35%.

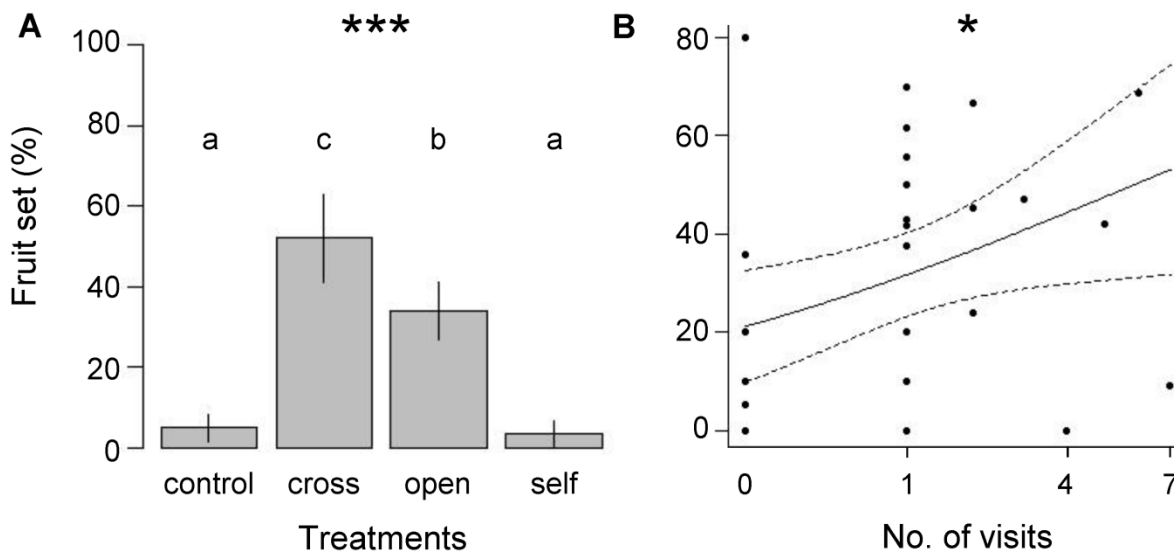


Figure 3. Pollen limitation. (A) Mean fruit set (% of flowers that developed into fruits) per pollination treatment. 'Control' flowers were bagged, 'cross' flowers were bagged and pollinated by hand with pollen from other trees, 'open' flowers had no treatment, and 'self' flowers were bagged and pollinated by hand with pollen from the same tree. Error bars indicate standard error of the mean. Overall significance of treatments on fruit set indicated with *** p<0.001. Different letters above bars

indicate significant differences between treatments at $p < 0.01$. **(B)** Mean fruit set of ‘open’ flowers per study site in relation to the number of flower visiting insects during 90 min of video observation (axis square root transformed). Results based on GLM (quasi-binomial error distribution). Solid lines show predicted values, dashed lines are estimated standard errors. Dispersion parameter = 2.8, residual df = 25, significance level: * $p < 0.05$.

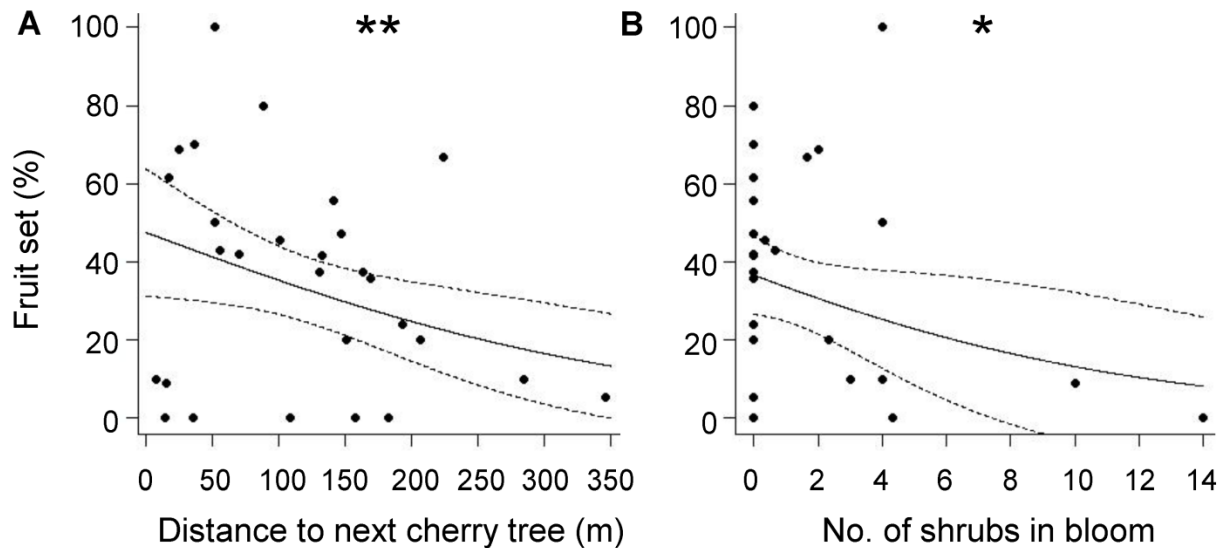


Figure 4. Pollination success. Mean fruit set of ‘open’ flowers per study site in relation to **(A)** distance to the next wild or cultivated cherry tree and **(B)** the number of shrubs in bloom around the study site (buffer 50 m). Results are based on best-fitting GLM (quasi-binomial error distribution) according to QAICc model selection. Solid lines show predicted values of best-fitting model, dashed lines are estimated standard errors. Dispersion parameter = 2.1, residual df = 24, significance levels: ** $p < 0.01$, * $p < 0.05$, explained deviance = 37%.

Supporting information

Table S1. Flower visitation. Visitor groups, total number of flower visits per group, and mean visit score per group derived from 90 min video observation per study site. For analysis, only pollinator groups with a mean visit score ≥ 2.5 were included (see Material and Methods for details). Nesting strategies of solitary bees are shown.

| Visitor Order | Group | No. of visits | Visit score | Analysis | Nesting |
|---------------|---------------------------|---------------|-------------|---------------------|----------|
| Hymenoptera | <i>Apis mellifera</i> | 6 | 3.0 | yes/no ¹ | |
| | <i>Andrena haemorrhoa</i> | 12 | 3.0 | yes | ground |
| | <i>Andrena cf gravida</i> | 4 | 2.5 | yes | ground |
| | <i>Andrena nitida</i> | 1 | 3.0 | yes | ground |
| | <i>Osmia bicornis</i> | 2 | 3.0 | yes | cavities |
| | Formicidae | 8 | 1.5 | no | |
| | Other | 20 | 2.0 | no | |
| Diptera | Empididae | 14 | 2.9 | yes | |
| | Syrphidae | 2 | 2.5 | yes | |
| | Other | 36 | 1.9 | no | |
| Coleoptera | | 21 | 1.7 | no | |
| Heteroptera | | 1 | 2.0 | no | |
| Total | | 127 | | | |

¹ Statistical models were calculated with and without domestic honey bees (see Results for details).

Table S2. Correlation-matrix of explanatory variables

| | Wood Amount | Cherry Isolation | Cherry Amount | OSNH ¹ | No of Shrubs | No of Cherry Flowers | Ground Flower Cover | Flowers per Video | Wind |
|----------------------|-------------|------------------|---------------|-------------------|---------------|----------------------|---------------------|-------------------|-------|
| Wood Isolation | -0.02 | 0.21 | 0.12 | 0.05 | -0.56* | 0.00 | -0.12 | -0.14 | 0.34 |
| Wood Amount | | 0.38* | -0.56* | -0.25 | -0.22 | 0.23 | 0.30 | 0.26 | -0.19 |
| Cherry Isolation | | | -0.40* | -0.14 | -0.39* | 0.21 | -0.02 | -0.27 | -0.00 |
| Cherry Amount | | | | -0.06 | 0.01 | -0.34 | -0.24 | -0.14 | 0.25 |
| OSNH ¹ | | | | | 0.16 | 0.02 | 0.10 | -0.12 | 0.34 |
| No of Shrubs | | | | | | -0.13 | 0.31 | 0.01 | -0.25 |
| No of Cherry Flowers | | | | | | | 0.23 | 0.46* | 0.15 |
| Ground Flower Cover | | | | | | | | 0.23 | -0.11 |
| Flowers per Video | | | | | | | | | 0.01 |

*Significant Pearson correlations at $p < 0.05$ in **bold**.

¹Open semi-natural habitats (non-woody)

Table S3. Best-fitting models explaining flower visitation according to AICc selection. The 'delta' column shows the difference between a model's AIC and that of the best-fitting model. Dark grey shaded line shows best-fitting model. Light grey shaded lines highlight models including correlated variables (in bold) instead of variables (x) present in the best-fitting model.

| Rank | Intercept | Wood Amount | Wood Isolation | Cherry Amount | Cherry Isolation | OSNH | No of Cherry Flowers | Ground Cover | Flower | No of Shrubs | Wind | Flower per Video | Wood Isolation | df | logLik | AICc | delta | weight |
|------|-----------|-------------|----------------|---------------|------------------|-------|----------------------|--------------|--------|--------------|-------|------------------|----------------|----|--------|-------|-------------|--------|
| 1 | 0.48 | 0.02 | | | -0.01 | | | | | | | | | 3 | -40.96 | 88.96 | 0.00 | 0.07 |
| 2 | 0.12 | 0.02 | | | -0.01 | | 0.02 | | | | | | | 4 | -39.72 | 89.26 | 0.30 | 0.06 |
| 3 | 1.42 | 0.03 | | | -0.01 | | 0.03 | | | | | | | 5 | -38.78 | 90.42 | 1.45 | 0.04 |
| 4 | 1.01 | 0.02 | | | -0.01 | | 0.02 | | | | -0.30 | | -0.65 | 5 | -38.81 | 90.47 | 1.51 | 0.04 |
| 5 | 0.20 | 0.03 | | | -0.01 | | | | 0.05 | | | | | 4 | -40.37 | 90.55 | 1.59 | 0.03 |
| 6 | 1.23 | 0.02 | | | -0.01 | | | | -0.23 | | | | | 4 | -40.39 | 90.59 | 1.63 | 0.03 |
| 7 | 0.41 | 0.02 | | | -0.01 | | | 0.01 | | | | | | 4 | -40.41 | 90.64 | 1.68 | 0.03 |
| 8 | -0.21 | 0.02 | | | -0.01 | | 0.02 | | 0.06 | | | | | 5 | -39.03 | 90.93 | 1.96 | 0.03 |
| 9 | 0.04 | 0.03 | | 0.01 | -0.01 | | | | | | | | | 4 | -40.57 | 90.95 | 1.98 | 0.03 |
| 10 | -0.51 | 0.03 | | 0.01 | -0.01 | | 0.02 | | | | | | | 5 | -39.08 | 91.02 | 2.05 | 0.03 |
| 11 | -1.47 | 0.04 | | 0.02 | -0.01 | | 0.02 | | 0.09 | | | | | 6 | -37.62 | 91.44 | 2.48 | 0.02 |
| 12 | 0.62 | 0.02 | | | -0.01 | -0.03 | | | | | | | | 4 | -40.89 | 91.59 | 2.63 | 0.02 |
| 13 | 0.68 | 0.02 | | | -0.01 | | | | | | | -0.09 | | 4 | -40.93 | 91.69 | 2.72 | 0.02 |
| 14 | 0.11 | 0.02 | | | -0.01 | | 0.02 | | 0.00 | | | | | 5 | -39.46 | 91.77 | 2.80 | 0.02 |
| 15 | -0.65 | 0.03 | | 0.02 | -0.01 | | | | 0.08 | | | | | 5 | -39.48 | 91.81 | 2.84 | 0.02 |
| 16 | 2.22 | 0.03 | | | -0.01 | | 0.03 | | | | -0.29 | | -0.62 | 6 | -37.92 | 92.04 | 3.08 | 0.02 |
| 17 | 0.79 | 0.03 | | 0.02 | -0.01 | | 0.03 | | | | | -0.74 | | 6 | -37.94 | 92.08 | 3.11 | 0.02 |
| 18 | 0.21 | 0.02 | | | -0.01 | -0.02 | 0.02 | | | | | | | 5 | -39.69 | 92.24 | 3.28 | 0.01 |
| 19 | 0.43 | 0.03 | | 0.01 | -0.01 | | 0.02 | | | | -0.32 | | | 6 | -38.05 | 92.30 | 3.33 | 0.01 |
| 20 | -0.22 | 0.03 | | 0.01 | -0.01 | | | 0.01 | | | | | | 5 | -39.73 | 92.32 | 3.35 | 0.01 |
| 21 | 0.82 | 0.03 | | 0.01 | -0.01 | | | | | | -0.27 | | | 5 | -39.84 | 92.54 | 3.57 | 0.01 |
| 22 | 1.11 | 0.02 | | | -0.01 | | | | 0.01 | | -0.22 | | | 5 | -39.92 | 92.69 | 3.73 | 0.01 |
| 23 | 1.01 | 0.03 | | | -0.01 | | 0.03 | | | 0.05 | | | | 6 | -38.30 | 92.81 | 3.85 | 0.01 |
| 24 | 0.82 | 0.02 | | | -0.01 | | | | 0.04 | | -0.17 | | | 5 | -40.11 | 93.08 | 4.12 | 0.01 |
| 25 | 1.41 | 0.03 | | | -0.01 | | 0.03 | | | | | -0.66 | | 6 | -38.47 | 93.15 | 4.18 | 0.01 |
| 26 | 0.24 | 0.02 | | | -0.01 | -0.04 | | 0.00 | | 0.04 | | | | 5 | -40.20 | 93.25 | 4.29 | 0.01 |
| 27 | 0.40 | 0.03 | | | -0.01 | | 0.02 | | 0.06 | | | | | 5 | -40.22 | 93.29 | 4.32 | 0.01 |
| 28 | 0.61 | 0.02 | | 0.02 | -0.01 | | 0.04 | | 0.04 | -0.24 | | | | 6 | -38.55 | 93.30 | 4.33 | 0.01 |
| 29 | -0.25 | 0.04 | | 0.02 | -0.01 | | 0.04 | | 0.08 | | | -0.69 | | 7 | -36.71 | 93.32 | 4.36 | 0.01 |
| 30 | -0.66 | 0.03 | | 0.02 | -0.01 | | 0.02 | | | | | | | 6 | -38.58 | 93.35 | 4.39 | 0.01 |
| 31 | 1.81 | 0.03 | | 0.02 | -0.01 | -0.04 | 0.03 | | | | | -0.72 | | 6 | -38.61 | 93.41 | 4.45 | 0.01 |
| 32 | 0.58 | 0.02 | | 0.02 | -0.01 | -0.03 | 0.02 | | | | | | | 5 | -40.31 | 93.48 | 4.52 | 0.01 |
| 33 | 0.96 | 0.02 | | 0.02 | -0.01 | | 0.02 | | -0.29 | | | | | 6 | -38.65 | 93.49 | 4.53 | 0.01 |
| 34 | 0.79 | 0.02 | | | -0.01 | | | 0.01 | | | | -0.17 | | 5 | -40.32 | 93.50 | 4.53 | 0.01 |
| 35 | 0.31 | 0.03 | | | -0.01 | | | 0.01 | 0.05 | | | -0.04 | | 5 | -40.36 | 93.58 | 4.62 | 0.01 |
| 36 | 1.25 | 0.02 | | | -0.01 | -0.01 | | | -0.23 | | | | | 5 | -40.38 | 93.62 | 4.65 | 0.01 |
| ... | | | | | | | | | | | | | | | | | | |
| 106 | -2.44 | 0.03 | | 0.03 | x | | 0.02 | | 0.15 | | | | | 5 | -42.18 | 97.22 | 8.25 | 0.00 |
| ... | | | | | | | | | | | | | | | | | | |
| 110 | 0.74 | x | | 0.00 | -0.01 | | 0.02 | | | | | | | 4 | -43.76 | 97.33 | 8.37 | 0.00 |

Explanation: Cherry isolation was correlated with cherry amount and no. of shrubs in bloom (Table S2). The best alternative models (including cherry amount or no of shrubs instead of cherry isolation) had both a delta-AICc value of 8.25 (model with rank 106). Wood amount was further correlated with cherry amount. The best alternative model (including cherry amount instead of wood amount) had a delta-AICc value of 8.37 (model with rank 110).

Table S4. Best-fitting models explaining cherry fruit set according to QAICc selection. The 'delta' column shows the difference between a model's AIC and that of the best-fitting model. Dark grey shaded line shows best-fitting model. Light grey shaded lines highlight models including correlated variables (in bold) instead of variables (x) present in the best-fitting model.

| Rank | Intercept | Wood Amount | Wood Isolation | Cherry Amount | Cherry Isolation | OSNH | No of Cherry Flowers | Ground Flower Cover | No of Shrubs | Wind | Wood Isolation | df | logLik | QAICc | delta | weight |
|------|-----------|-------------|----------------|---------------|------------------|-------|----------------------|---------------------|--------------|------|----------------|----|--------|-------|-------------|--------|
| 1 | 0.64 | | | | -0.01 | | | | -0.25 | | | 3 | -59.88 | 48.54 | 0.00 | 0.11 |
| 2 | -0.26 | | | | -0.01 | | | | -0.25 | 0.24 | | 4 | -56.34 | 49.37 | 0.83 | 0.07 |
| 3 | 0.60 | | | | -0.01 | | | | -0.27 | | | 4 | -57.41 | 50.06 | 1.52 | 0.05 |
| 4 | 0.22 | | | 0.01 | -0.01 | | | 0.00 | -0.25 | | | 4 | -58.37 | 50.55 | 2.01 | 0.04 |
| 5 | 0.51 | 0.00 | | | -0.01 | | | | -0.25 | | | 4 | -59.51 | 51.29 | 2.75 | 0.03 |
| 6 | 0.75 | | | | -0.01 | -0.02 | | | -0.25 | | | 4 | -59.79 | 51.47 | 2.93 | 0.03 |
| 7 | 0.69 | | | | -0.01 | | 0.00 | | -0.25 | | | 4 | -59.86 | 51.52 | 2.97 | 0.02 |
| 8 | -0.62 | 0.02 | | 0.02 | -0.01 | | | | -0.22 | | | 5 | -55.75 | 52.13 | 3.58 | 0.02 |
| 9 | -0.62 | 0.01 | | | -0.01 | | | | -0.24 | 0.28 | | 5 | -55.47 | 52.15 | 3.60 | 0.02 |
| 10 | -0.38 | | | 0.01 | -0.01 | | | | -0.25 | 0.19 | | 5 | -55.59 | 52.22 | 3.68 | 0.02 |
| 11 | -0.23 | | | | -0.01 | -0.07 | | | -0.23 | 0.32 | | 5 | -55.63 | 52.25 | 3.71 | 0.02 |
| 12 | 0.09 | | | 0.01 | -0.01 | | | 0.01 | -0.27 | | | 5 | -55.79 | 52.36 | 3.81 | 0.02 |
| 13 | -1.53 | | | | 0.00 | | | | 0.41 | | | 3 | -65.69 | 52.39 | 3.84 | 0.02 |
| 14 | -0.31 | | | | -0.01 | | | 0.00 | -0.25 | 0.25 | | 5 | -56.24 | 52.65 | 4.10 | 0.01 |
| 15 | -0.24 | | | | -0.01 | | 0.00 | | -0.25 | 0.24 | | 5 | -56.34 | 52.71 | 4.17 | 0.01 |
| 16 | -2.22 | | | | -0.01 | | | | 0.44 | | | 2 | -70.98 | 53.04 | 4.50 | 0.01 |
| 17 | 0.46 | 0.01 | | | -0.01 | | | 0.00 | -0.26 | | | 5 | -56.89 | 53.07 | 4.52 | 0.01 |
| 18 | -0.10 | | | | -0.01 | | | | -0.27 | | | 2 | -71.14 | 53.11 | 4.56 | 0.01 |
| 19 | 0.75 | | | | -0.01 | -0.03 | | 0.00 | -0.27 | | | 5 | -57.25 | 53.30 | 4.76 | 0.01 |
| 20 | -1.08 | | | 0.02 | x | | | | -0.15 | | | 3 | -67.38 | 53.40 | 4.86 | 0.01 |
| 21 | 0.62 | | | | -0.01 | | 0.00 | 0.00 | -0.27 | | | 5 | -57.41 | 53.40 | 4.86 | 0.01 |
| 22 | -1.23 | | | 0.02 | | | | | -0.13 | 0.38 | | 2 | -72.00 | 53.66 | 5.12 | 0.01 |
| 23 | -1.85 | | | | | | | | | | | 3 | -67.69 | 53.69 | 5.14 | 0.01 |
| 24 | -1.64 | 0.02 | | 0.03 | 0.00 | | | | | | | 4 | -63.31 | 53.76 | 5.21 | 0.01 |
| 25 | -2.22 | 0.02 | | 0.03 | x | | | | | | | 3 | -67.93 | 53.76 | 5.21 | 0.01 |
| 26 | 0.09 | | | 0.01 | -0.01 | | 0.00 | | -0.24 | | | 5 | -58.27 | 53.76 | 5.22 | 0.01 |
| 27 | 0.24 | | | 0.01 | -0.01 | 0.00 | | | -0.25 | | | 5 | -58.36 | 53.82 | 5.28 | 0.01 |
| 28 | -2.25 | | | 0.01 | | | | | | 0.33 | | 3 | -68.03 | 53.90 | 5.36 | 0.01 |
| 29 | -1.33 | | | | -0.01 | -0.12 | | | 0.54 | | | 4 | -63.37 | 53.92 | 5.38 | 0.01 |
| 30 | -1.43 | 0.02 | | 0.02 | -0.01 | | | | -0.22 | 0.23 | | 6 | -52.58 | 53.97 | 5.42 | 0.01 |
| 31 | -3.40 | 0.02 | | 0.03 | | | | | 0.36 | | | 4 | -63.55 | 54.04 | 5.50 | 0.01 |
| 32 | -1.98 | 0.01 | | | -0.01 | | | | 0.46 | | | 4 | -63.57 | 54.05 | 5.51 | 0.01 |
| 33 | -0.61 | | | 0.01 | 0.00 | | | | | | | 3 | -68.71 | 54.27 | 5.72 | 0.01 |
| 34 | -1.84 | | | 0.02 | | | | | -0.15 | 0.25 | | 4 | -63.99 | 54.33 | 5.78 | 0.01 |
| 35 | -2.85 | 0.02 | | 0.02 | 0.00 | | | | 0.37 | | | 5 | -58.94 | 54.40 | 5.85 | 0.01 |
| 36 | 0.60 | 0.01 | | | -0.01 | | 0.00 | | -0.25 | | | 5 | -59.38 | 54.48 | 5.93 | 0.01 |
| 37 | -0.63 | 0.02 | | 0.02 | -0.01 | | | 0.00 | -0.24 | | | 6 | -53.41 | 54.51 | 5.96 | 0.01 |
| 38 | 0.60 | 0.00 | | | -0.01 | -0.02 | | | -0.25 | | | 5 | -59.46 | 54.53 | 5.99 | 0.01 |
| 39 | -1.80 | | | 0.02 | | | | | x | | | 4 | -64.56 | 54.56 | 6.02 | 0.01 |
| 40 | -0.06 | | | | 0.00 | | 0.00 | | | | | 3 | -69.11 | 54.61 | 6.06 | 0.01 |

Cherry isolation was correlated with cherry amount and wood amount (Table S2). The best alternative models (including cherry amount or wood amount instead of cherry isolation) had a delta-AICc value of 4.86 and 5.21, respectively (models with ranks 20 and 25). No of shrubs was further correlated with wood isolation. The best alternative model (including wood isolation instead of no. of shrubs) had a delta-AICc value of 6.02 (model with rank 39).

Chapter 4:**Wild pollinators enhance fruit set of crops regardless of honey bee abundance****Information**

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Abstract

Diversity and abundance of wild-insect pollinators have declined in many agricultural landscapes. Whether such declines reduce crop yields, or are mitigated by managed pollinators such as honey bees, is unclear. Here we show universally positive associations of fruit set with wild-insect visits to flowers in 41 crop systems worldwide, and thus clearly demonstrate their agricultural value. In contrast, fruit set increased significantly with visitation by honey bees in only 14% of the systems surveyed. Overall, wild insects pollinated crops more effectively, because increase in their visitation enhanced fruit set by twice as much as an equivalent increase in honey bee visitation. Further, visitation by wild insects and honey bees promoted fruit set independently, so high abundance of managed honey bees supplemented, rather than substituted for, pollination by wild insects. Our results suggest that new practices for integrated management of both honey bees and diverse wild-insect assemblages will enhance global crop yield.

Introduction

Human persistence depends on many natural processes, termed ecosystem services, which are usually not accounted for in market valuations. Global degradation of such services can undermine the ability of agriculture to meet the demands of the growing, increasingly affluent, human population (Tilman et al. 2001, Roberts 2011). Pollination of crop flowers provided by wild insects is one such vulnerable ecosystem service (Klein et al. 2007), as their abundance and diversity are declining in many agricultural landscapes (Potts et al. 2010, Garibaldi et al. 2011b). Globally, yields of insect-pollinated crops are often managed for greater pollination through the addition of honey bees (*Apis mellifera* L.) as an agricultural input (Fig. 1) (Morse 1991, Goodwin et al. 2011, Rucker et al. 2012). Therefore, the potential impact of declines in wild pollinators on crop yields is largely unknown, as is whether increasing application of honey bees (Aizen and Harder 2009) compensates for losses of wild pollinators, or even promotes these losses.

Wild insects may increase the proportion of flowers that develop into mature fruits or seeds (fruit set), and therefore crop yield (e.g., Kg ha⁻¹, Fig. S1), by contributing to pollinator abundance, species number (richness), and (or) equity in relative species abundance (evenness). Increased pollinator abundance, and therefore visitation rate to crop flowers, should augment fruit set at a decelerating rate until additional individuals do not further increase (e.g., pollen saturation), or even decrease (e.g., pollen excess) fruit set (Chacoff et al. 2008, Morris et al. 2010, Garibaldi et al. 2011a). Richness of pollinator species should increase the mean, and reduce the variance, of fruit set (Winfree and Kremen 2009), because of complementary pollination among species (Hoehn et al. 2008, Blüthgen and Klein 2011), facilitation (Greenleaf and Kremen 2006, Carnevalheiro et al. 2011), or “sampling effects” (Cardinale et al. 2006), among other mechanisms (Tscharntke et al. 2005, Klein et al. 2009). Pollinator evenness may enhance fruit set via complementarity, or diminish it if a dominant species (e.g., honey bee) is the most effective pollinator (Hillebrand et al. 2008). To date, the few studies on the

importance of pollinator richness for crop pollination have revealed mixed results (Cardinale et al. 2012), the effects of evenness on pollination services remain largely unknown, and the impact of wild-insect loss on fruit set has not been evaluated globally for animal-pollinated crops.

We tested four predictions arising from the assumption that wild insects effectively pollinate a broad range of crops, and that their role can be re-placed by increasing the abundance of honey bees in agricultural fields: (1) for most crops, wild-insect and honey bee visitation enhances pollen deposition on stigmas of flowers; (2) consequently, for most crops, wild-insect and honey bee visitation improves fruit set; (3) visitation by wild insects promotes fruit set only when honey bees visit infrequently (i.e., negatively interacting effects between wild-insect visitation and honey bee visitation); and (4) pollinator assemblages with more species benefit fruit set only when honey bees visit infrequently (i.e., negatively interacting effects between richness and honey bee visitation).

Material and methods

To test these predictions we collected data at 600 fields on all continents, except Antarctica, for 41 crop systems (Fig. 1). Crops included a wide array of animal-pollinated, annual and perennial fruit, seed, nut, and stimulant crops; predominately wind-pollinated crops were not considered (Fig. S2 and Table S1). Sampled fields were subject to a diversity of agricultural practices, ranging from extensive monocultures to small and diversified systems (Fig. S2 and Table S1), fields stocked with low to high densities of honey bees (Fig. 1 and Table S2), and fields with low to high abundance and diversity of wild insects (Fig. S3 and Table S2). For each field, we measured flower visitation per unit of time (hereafter “visitation”) for each insect species, from which we estimated species richness and evenness (see supplementary materials). We quantified pollen deposition for 14 systems as the number of pollen grains per stigma, and fruit set (a key component of crop yield, Fig. S1) for 32 systems as the percentage of flowers setting mature fruits or seeds. Spatial or temporal variation of pollen deposition and fruit set were measured as the coefficient of variation (CV) over sample points or days within each field (Garibaldi et al. 2011a). The multilevel data provided by fields within systems were analysed with general linear mixed-effects models that included crop system as a random effect, and wild-insect visitation, honey bee visitation, evenness, richness, and all their interactions as fixed effects. Best-fitting models were selected based on Akaike’s Information Criterion (AIC) (see supplementary materials).

Results and discussion

In agreement with the first prediction, crops in fields with more flower visits received more pollen on stigmas, with an overall 74% stronger influence of visitation by honey bees than by wild insects (Fig. 2A and Table S3). Honey bee visitation significantly increased pollen deposition (i.e., confidence intervals for individual regression coefficients, β_i , do not include zero) in seven of ten crop systems,

and wild insects in ten of 13 systems (Fig. S4). Correspondingly, increased wild-insect and honey bee visitation reduced variation in pollen deposition among samples (Fig. S5).

Contrary to the second prediction, fruit set increased significantly with wild-insect visitation in all crop systems, but with honey bee visitation in only 14% of systems (Fig. 2B). In addition, fruit set increased twice as strongly with visitation by wild insects than by honey bees (Fig. 2A). These partial regression coefficients did not differ simply because of unequal abundance, or disparate variation in visitation between wild insects and honey bees. In crop systems visited by both honey bees and wild insects, honey bees accounted for half of the visits to crop flowers (mean = 51%; CI95% = 40-62%), and among-field CVs for visitation by honey bees (mean = 73%; CI95% = 57-88%) and by wild insects (mean = 79%; CI95% = 62-96%) were equivalent. Furthermore, wild-insect visitation had stronger effects than honey bee visitation, regardless of whether honey bees were managed or feral (Fig. S6) and, comparing across systems, even where only wild insects or honey bees occurred (Fig. 2B). Moreover, wild-insect visitation alone predicted fruit set better than honey bee visitation alone ($\Delta AIC = 16$, model F vs. M in Table S4). Correspondingly, the CV of fruit set decreased with wild-insect visitation, but varied independently of honey bee visitation (Fig. S5).

Pollinator visitation affected fruit set less strongly than pollen deposition on stigmas (compare regression coefficients in Fig. 2A). This contrast likely arose from pollen excess, filtering of pollen tubes by post-pollination processes, and (or) seed abortion (Aizen and Harder 2007, Chacoff et al. 2008), and so reflects pollination quality, in part. Intriguingly, the difference in coefficients between pollen deposition and fruit set for honey bees greatly exceeds that for wild insects (Fig. 2A), indicating that wild insects provide better quality pollination, such as greater cross-pollination (Greenleaf and Kremen 2006, Hoehn et al. 2008, Klein et al. 2009, Carvalheiro et al. 2011). These results occurred regardless of which crop systems were selected (Fig. S7), sample size (Fig. S8), the relative frequency of honey bees in the pollinator assemblage (dominance) among systems, the pollinator dependence of crops, or whether the crop species were herbaceous or woody, or native or exotic (Fig. S9). Poor-quality pollination could arise if insect foraging behaviour, based on focal resources typical of honey bees (Greenleaf and Kremen 2006, Carvalheiro et al. 2011), causes pollen transfer between flowers of the same plant individual or the same cultivar within a field, thereby limiting cross-pollination and increasing the incidence of self-pollen interference and inbreeding depression (Aizen and Harder 2007). The smaller difference in coefficients between pollen deposition and fruit set for wild insects, and the stronger effect on fruit set of wild-insect visitation, suggest that management to promote diverse wild insects has great potential to improve global yield of animal-pollinated crops.

The third prediction was also not supported, as fruit set increased consistently with visitation by wild insects, even where honey bees visited frequently (i.e., no statistical interaction: Fig. 2, A and C). In particular, the best-fitting model (lowest AIC) for fruit set included additive effects of both visitation by wild insects and honey bees (model P in Table S4), suggesting that managed honey bees supplement the pollination service of wild insects, but cannot replace it. Overall, visitation by wild

insects and honey bees were not correlated among fields (Fig. S10), providing no evidence for either competition for the resources obtained from crop flowers (pollen, nectar), or density compensation (Winfree and Kremen 2009) between wild insects and honey bees at the field scale. Even if honey bees displace wild insects (or vice-versa) at the flower scale (Greenleaf and Kremen 2006, Carvalheiro et al. 2011), this is unlikely to scale up to the field, as indicated by our data, if mass-flowering crops provide floral resources in excess of what can be exploited by local pollinator populations. Therefore, although insect pollinators appear not to be limited by crop floral resources, yield was commonly pollen limited, as crops set more fruit in fields with more visitation by pollinators (Fig. 2).

Contrary to the fourth prediction, fruit set increased with flower-visitor richness independently of honey bee visitation (Fig. S11). Correspondingly, the CVs of fruit set decreased with richness; in contrast, evenness did not affect the mean or CV of fruit set (Figs S12 and S13). Visitation by wild insects increased strongly with richness (Fig. 3), and improved model fit (lower AIC), even when richness was included in the model (model B vs. G in Table S4). However, richness did not enhance model fit when added to a model with wild-insect visitation (model F vs. G in Table S4), suggesting that the effects of richness on fruit set reflect increased wild-insect visitation (i.e., co-linear effects: Fig. S13). Like wild-insect visitation (Fig. S10), richness did not correlate with honey bee visitation (Table S5). Previous studies have shown that agricultural intensification reduces both species richness of pollinator assemblages and wild-insect visitation (Klein et al. 2009, Winfree and Kremen 2009, Potts et al. 2010, Garibaldi et al. 2011b). Our results for multiple crop systems further demonstrate that fields with fewer species experience less visitation by wild insects and reduced fruit set, independent of species evenness or honey bee visitation. Globally, wild-insect visitation signals both species richness and pollination services, and is a relatively inexpensive indicator that can be standardized easily among observers in field samples (Kremen et al. 2011).

Conclusions

Large, active colonies of honey bees provide abundant pollinators that can be moved as needed, hence their appeal for pollination management in most animal-pollinated crops (Morse 1991, Delaplane and Mayer 2000, Goodwin et al. 2011, Rucker et al. 2012). By comparison, methods for maintaining diverse wild insects for crop pollination are less developed, and research on such pollination services is more recent (Delaplane and Mayer 2000, Tscharrntke et al. 2005, Greenleaf and Kremen 2006, Klein et al. 2007, Kremen et al. 2007, Carvalheiro et al. 2011) (Table S1). Although honey bees are generally viewed as a substitute for wild pollinators (Morse 1991, Klein et al. 2007, Goodwin et al. 2011, Rucker et al. 2012), our results demonstrate that they neither maximize pollination, nor fully replace the contributions of diverse, wild-insect assemblages to fruit set for a broad range of crops and agricultural practices on all continents with farmland. These conclusions hold even for crops stocked routinely with high densities of honey bees for pollination, such as almond, blueberry or watermelon (Fig. 2 and Table S2). Dependence on a single species for crop pollination also carries the risks

associated with predator, parasite and pathogen development (Tscharntke et al. 2005, Winfree et al. 2007b, Potts et al. 2010). Our results support integrated management policies (Aebi et al. 2012) that include pollination by both wild insects as ecosystem service providers, and managed species, such as honey bees, bumble bees (*Bombus* spp.), leafcutter bees (*Megachile* spp.), mason bees (*Osmia* spp.), and stingless bees (*Meliponini*) as agricultural inputs (where they are not invasive species). Such policies should include conservation or restoration of natural or semi-natural areas within croplands, promotion of land-use heterogeneity (patchiness), addition of diverse floral and nesting resources, and consideration of pollinator safety as it relates to pesticide application (Tscharntke et al. 2005, Greenleaf and Kremen 2006, Klein et al. 2007, Kremen et al. 2007, Carvalheiro et al. 2011). Some of these recommendations entail financial and opportunity costs, but the benefits of implementing them transcend the supply of pollination services alone and extend to, for example, mitigation against soil erosion, and improved pest control, nutrient cycling and water use efficiency (Wratten et al. 2012). Without such changes, the on-going loss of wild insects (Potts et al. 2010, Garibaldi et al. 2011b) is destined to compromise agricultural yields worldwide.

Figures

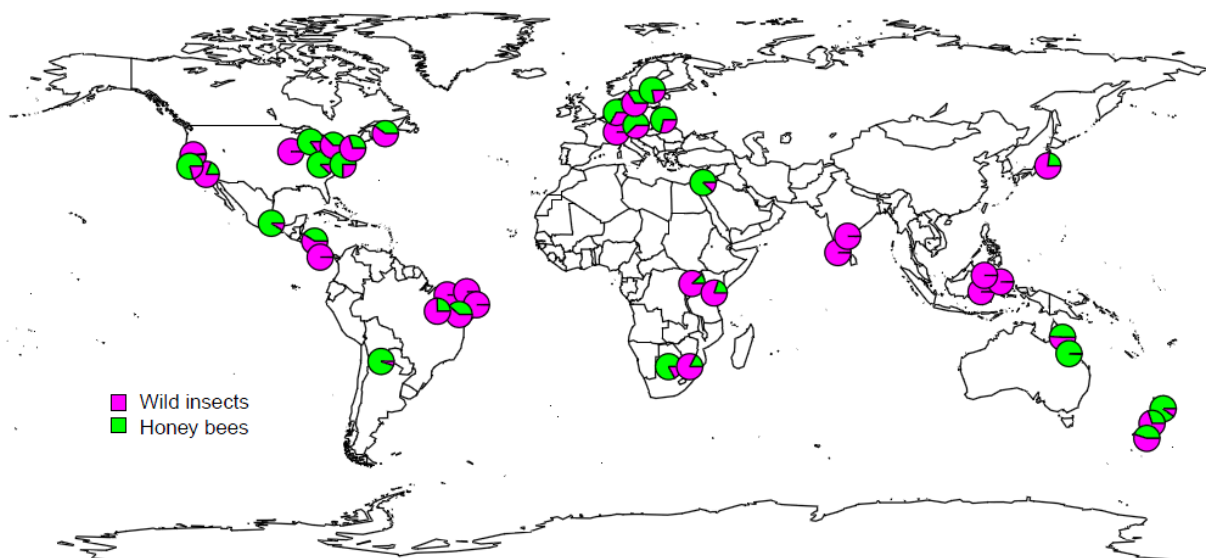


Figure 1. Locations of the 41 crop systems studied. Symbols indicate the percentage of total visitation rate to crop flowers contributed by honey bees (*Apis mellifera* L.) and wild insects. Honey bees occur as domesticated colonies in transportable hives worldwide, as a native species in Europe (rarely) and Africa, or as feral populations in all other continents, except Antarctica.

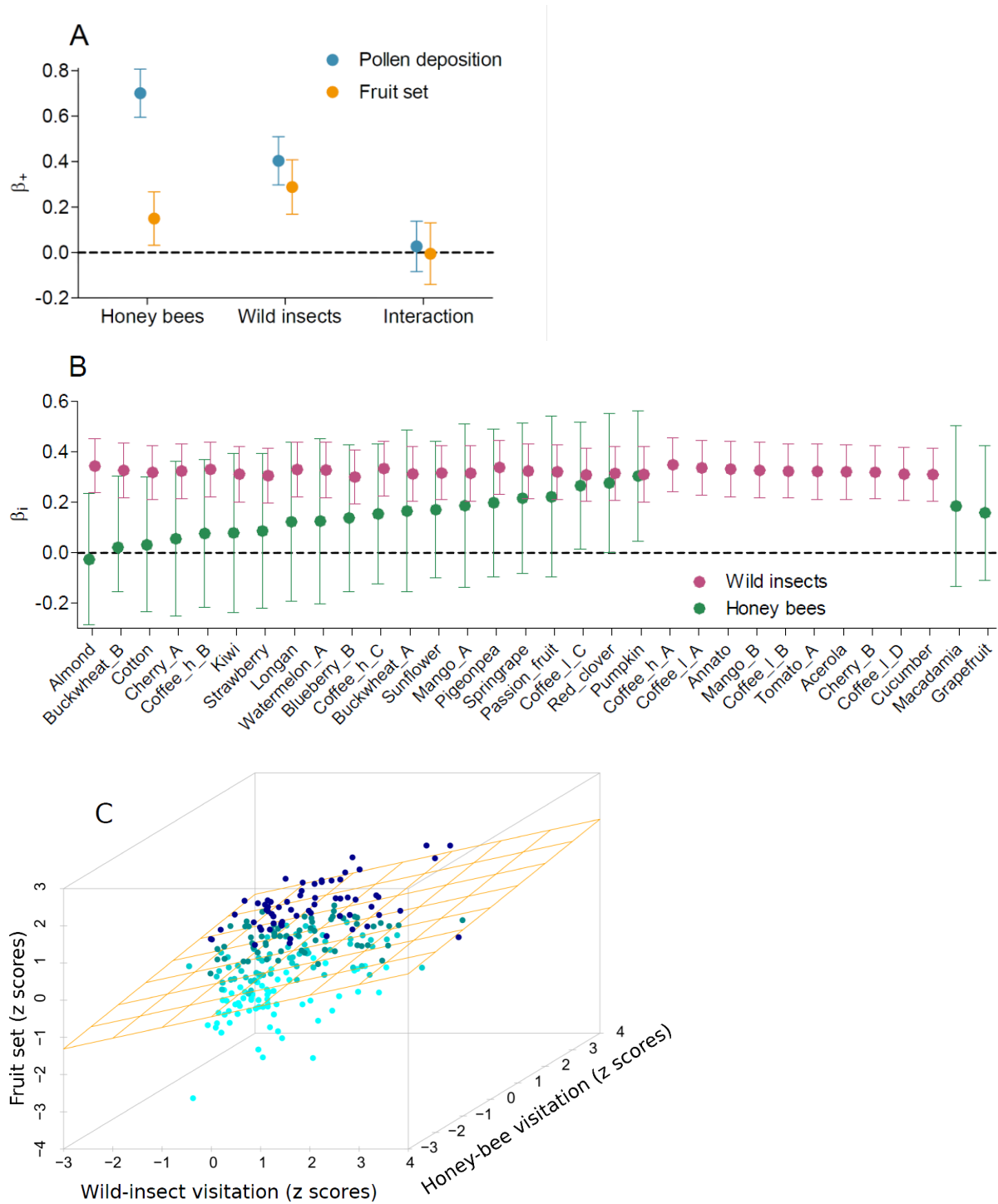


Figure 2. Visitation rate to crop flowers by wild insects enhances reproduction in all crops examined (regression coefficient, $\beta_i > 0$), whereas honey bee visitation has weaker effects overall. **(A)** Overall partial regression coefficients ($\beta_+ \pm 95\%$ confidence interval) for the direct and interacting effects of visitation by wild insects and honey bees on pollen deposition or fruit set (models R and Q in Tables S3 and S4, respectively). **(B)** Slopes ($\beta_i \pm 95\%$ confidence interval) represent the effects of visitation by wild insects or honey bees on fruit set for individual crop systems. Cases on the right are systems in which only wild insects or only honey bees were present. Data from individual crop systems were

standardized by z-scores prior to analysis, permitting comparison of regression coefficients in all panels. Letters after the crop name indicate different regions (Table S1), for example Mango_A and Mango_B are located in South Africa and Brazil, respectively. (C) Given the absence of interaction between the effects of visitation by wild insects and honey bees, maximum fruit set is achieved with high visitation by both wild insects and honey bees (upper right side of the figure). The plane in orange is the overall regression (model P in Table S4: the inclination of the surface in the y and x directions reflects the β_+ for visitation of wild insects and honey bees, respectively), and each point is a field in a crop system (fruit set increases from cyan to dark blue).

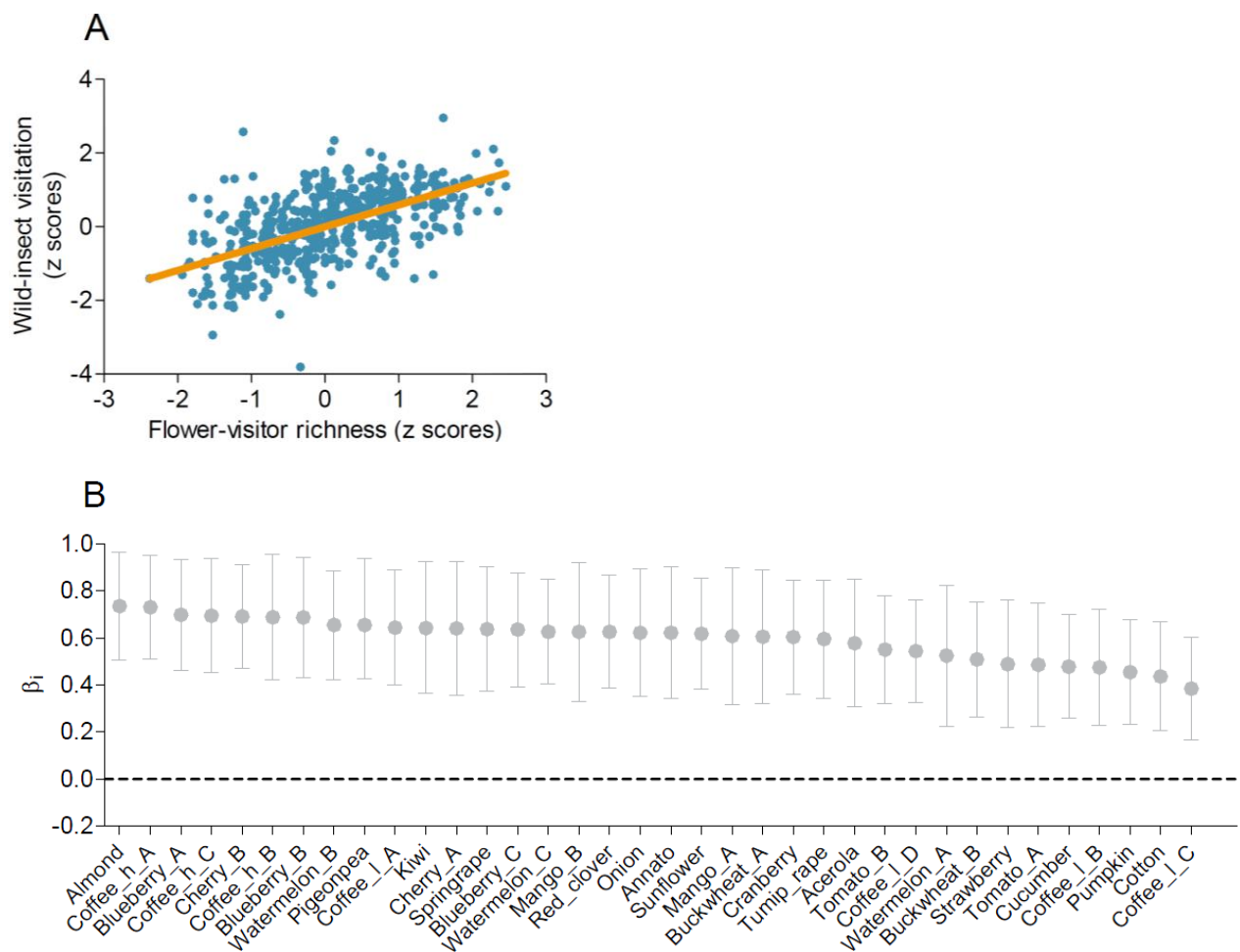


Figure 3. Globally, visitation rate to crop flowers by wild insects increases with flower-visitor richness. (A) The line is the overall regression, and each point is a field in a crop system. (B) Slopes ($\beta_i \pm 95\%$ confidence interval) represent the effect of richness on wild-insect visitation for individual crop systems. Data from individual crop systems were standardized by z-scores prior to analysis (after log-transformation for visitation), permitting direct comparison of regression coefficients.

Chapter 5:

Habitat isolation affects plant-herbivore-enemy interactions on cherry trees

Information

This chapter will be submitted as:

Schüepp C., Uzman D., Herzog F., Entling M.H. Habitat isolation affects plant-herbivore-enemy interactions on cherry trees.

Author contributions: CS, FH and MHE designed experiment, CS and DU performed experiment, CS and MHE analysed data and wrote manuscript.

Abstract

Understanding mechanisms behind suppression of herbivores by natural enemies is essential for the successful implementation of natural pest control. Studies including multiple enemies affecting multiple herbivores, crop damage, and plant growth are needed. Here, we investigated plant-herbivore-enemy interactions on young cherry trees, separating independent effects of (1) isolation of cherry trees from the next woody habitat and (2) the amount of woody habitat in the surrounding landscape. The isolation of studied cherry trees affected most enemies negatively. Herbivores were either positively affected by isolation or showed no response. In contrast, the amount of woody habitat in the landscape was not relevant for herbivore-enemy interactions. Plant growth was affected by bottom-up (nutrient availability) and top-down (aphid density) forces but did not change significantly with habitat amount or isolation. Herbivore densities decreased more strongly with enemy diversity than with the density of single enemy groups. Some enemies were even positively correlated with herbivore density, indicating that they were bottom-up controlled rather than controlling their prey. In conclusion, we found correlative evidence that emerging (additive or synergistic) effects of multiple predators controlled herbivores on cherry trees. Further, herbivores were partially released from enemy suppression at isolated sites, in accordance with the hypothesis that habitat connectivity improves pest control. Effects of habitat isolation on aphids and tree growth observed three years earlier on the same trees did not recur. This suggests that fragmentation effects in perennial habitats change over time and underpins the importance of long-term experiments.

Key words

Biodiversity-ecosystem functioning, biological pest control, bottom-up versus top-down, cherry tree *Prunus avium*, landscape composition versus configuration, habitat loss versus fragmentation *per se*, productivity.

Introduction

NATURAL PEST CONTROL AND PLANT GROWTH

Plant growth is expected to be promoted by predators reducing herbivores, but the presence of natural enemies does not necessarily translate into suppression of herbivores and increased plant performance (Chaplin-Kramer et al. 2011). The delivery of an ecosystem service like pest control depends not only on the density of service providers but also on their effectiveness (Kremen 2005): First, predation of herbivores is positively correlated with herbivore densities in some systems (Thies et al. 2005), suggesting that herbivore density may drive enemy populations rather than *vice versa* (Chaplin-Kramer et al. 2011). Second, herbivores may be controlled by the availability and distribution of their resources rather than by enemy suppression (Bengtsson 2010, Chaplin-Kramer et al. 2011). Third, multiple predators may negatively interact with each other (Snyder et al. 2006, Martin et al. 2013). And fourth, the effectiveness of herbivore control may depend much more on the presence of specific, highly effective species rather than on total density of predator groups (Straub and Snyder 2006, Philpott et al. 2009). Therefore, the ecosystem service of pest control is more adequately measured as plant damage and growth rather than only as density of enemies, but studies measuring plant damage and growth are still rare (Chaplin-Kramer et al. 2011, Veres et al. 2013). Further, it is necessary to include multiple predators in one study to understand additive or synergistic effects emerging in the presence of multiple predators (Losey and Denno 1998, Sih et al. 1998). In addition to negative effects by herbivores, plant growth is largely dependent on the availability of nutrients (Throop 2005, Zehnder and Hunter 2008). Therefore, integrating both bottom-up and top-down forces is necessary to understand the relative importance of each factor for plant growth (Hunter and Price 1992, Hooper et al. 2005, Müller et al. 2005).

LANDSCAPE EFFECTS

Herbivores and their enemies are often mobile organisms influenced by the distribution of resources in the landscape (Kremen et al. 2007, Tscharntke et al. 2012). Therefore, plant growth may not only depend on local but also on landscape factors. Density of herbivores on crops can be affected by the landscape either indirectly by a spillover of natural enemies from adjacent (semi-) natural habitat into agricultural fields (Tscharntke et al. 2005, Bianchi et al. 2006, Tscharntke et al. 2007, Eilers and Klein 2009, Chaplin-Kramer and Kremen 2012), or directly because herbivores themselves develop in these habitats and disperse from there (Thies et al. 2005, Martin et al. 2013). Therefore, positive effects of landscape complexity on enemies may be counteracted by positive effects on herbivores (Roschewitz et al. 2005). Many metrics are used to evaluate the effect of landscape complexity on pest control (Chaplin-Kramer et al. 2011). The percentage of (semi-) natural habitat surrounding study sites is a metric that can be consistently used and should therefore be preferred (Chaplin-Kramer et al. 2011). However, the amount of habitat at the landscape scale is often correlated with measures of habitat fragmentation such as isolation (Fahrig 2003). Experimental evidence for the effects of both habitat

isolation and amount is needed to design agricultural landscapes that support biodiversity and ecosystem services (Tschamntke et al. 2007, Hadley and Betts 2012, Tschamntke et al. 2012). The amount of suitable habitat determines the pool of available species and individuals in a given landscape, whereas habitat isolation constrains access to this species pool (Tschamntke et al. 2012).

IMPORTANCE OF WOODY HABITAT

Semi-natural habitat including woody elements such as hedgerows, tree lines, traditional orchards, forest edges and forests promote biodiversity in agricultural landscapes (Dix et al. 1995, Attwood et al. 2008, Billeter et al. 2008, Diekötter and Crist 2013). They provide suitable conditions for breeding and hibernation or continuous supply of hosts, prey, pollen or nectar for the majority of species (Corbett and Rosenheim 1996, Landis et al. 2000, Duelli and Obrist 2003, Kells and Goulson 2003, Pywell et al. 2005, Bianchi et al. 2006) or serve as connectivity elements (Wamser et al. 2012). Heterogeneous landscapes have more crop to non-crop interfaces and allow colonization of crops by natural enemies (Bianchi and Van der Werf 2003). Ladybeetles colonise aphid-infested plants from their hibernation sites in non-crop habitat such as hedgerows and forests (Bianchi and Van der Werf 2003, Thomson and Hoffmann 2013). Woodlots are a source of spiders and parasitic wasps controlling leafhopper pests in vineyards (Corbett and Rosenheim 1996, Isaia et al. 2006b, Hogg and Daane 2010). Cavity-nesting predatory wasps are negatively affected by the isolation from woody habitat and the loss of woody habitat at the landscape scale (Schüepp et al. 2011). Hedgerows provide high quality overwintering habitat for spiders and predatory beetles (Pywell et al. 2005). And arthropods and birds on fruit trees depend particularly on woody semi-natural habitat such as forest, hedgerows or traditional orchards (Bailey et al. 2010).

HYPOTHESES

Here, we study effects of resource availability and the surrounding landscape on a tri-trophic system of cherry trees, multiple herbivores and their natural enemies. We hypothesised that:

1. Density and richness of natural enemies decrease with increasing isolation from woody habitat and with decreasing amounts of woody habitat in the landscape.
2. Density of herbivores increase with habitat isolation and with decreasing amounts of woody habitat because of lower enemy suppression.
3. Plant growth decreases with increasing habitat isolation and with decreasing amounts of woody habitat because of higher herbivory.

Materials and methods

STUDY SITES

The study was conducted in 2012 in the Swiss plateau between the cities of Bern, Solothurn, and Fribourg, where agricultural areas are interspersed with forest. We used spatially separated landscape

sectors distributed over an area of 23 by 32 km and varying in altitude between 465 and 705 m above sea level. The 30 experimental sites in the centre of each landscape sector consisted of 18-m-long rows of seven 8-years-old wild cherry trees (*Prunus avium* L.). Trees had been planted in 2008 on permanent grassland for the experiment and since then managed in a standardised manner (see Farwig et al. 2009, Schüepp et al. 2011). The sites were selected according to their percentage of woody habitat cover in a 500 m radius and their level of isolation from woody habitat. We chose the landscape scale of 500 m radius because many studies find enemy and pest responses at scales of 300 to 1000 m (Chaplin-Kramer et al. 2011, Martin et al. 2013). Woody habitat comprised hedgerows, orchards, single-standing trees, treelines, and forest. The percentage of these habitat types in a 500-m radius around the sites varied from 4 to 74%. Isolation had three levels: ten of the sites were located at the edge of forest (adjacent), ten in a distance of 100 - 200 m from the next forest edge but directly beside small-sized woody habitat such as hedgerows or trees (connected), and ten at the same distance from forest but isolated from any woody habitat by 100 - 200 m (isolated). Information on woody habitat was derived from official digital land-use maps (vector25, swisstopo, Wabern) and verified using aerial photographs and field inspection. Sites with different levels of isolation and with different percentages of woody habitat in the surrounding landscape were spatially interspersed ($p > 0.19$ for relationships of x and y coordinates with isolation and percentage of woody habitat, respectively).

HERBIVORES, MUTUALISTS AND ENEMIES

Because of rapid population growth of aphids early in the season and emigration of winged morphs to secondary hosts in June (Stutz and Entling 2011), predation early in the season is essential to prevent aphids from reaching levels that damage plants (Ekbom et al. 1992, Gardiner et al. 2009). On our studied trees, also herbivorous beetles were observed in highest numbers in early summer in earlier years (personal observations). Therefore, we sampled herbivores and their enemies on cherry trees once per month in May and June 2012. On each tree, we counted and determined arthropods to the lowest taxonomic level possible in the field. Several branches per tree with a total length of approximately 2 m were surveyed, using different branches in May and June. Additionally, cardboard rolls were attached to the stems in order to assess nocturnal arthropods or those living under the bark (Isaia et al. 2006a). We grouped herbivores into aphids (Aphidinae: *Myzus cerasi*) and beetles (Curculionidae: *Phyllobius* sp.; Scarabaeidae: *Phyllopertha* sp.). Enemies of aphids were grouped into hoverflies (Syrphidae: eggs and larvae), ladybeetles (Coccinellidae: eggs, larvae, and adults), earwigs (Forficulidae: *Forficula auricularia*), free-hunting spiders (Anyphaenidae, Clubionidae, Philodromidae, and Salticidae), web-building spiders (Araneidae, Dictynidae, Linyphiidae, Tetragnathidae, and Theridiidae), and predatory beetles (Cantharidae). Enemies of herbivorous beetles were grouped into spiders eating large prey (Araneidae: *Araniella* sp. *Nuctenea umbratica*, Clubionidae: *Clubiona* sp., Salticidae: *Marpissa* sp.), ants (Formicidae) and predatory beetles (Cantharidae). Because all observed ants were aphid-tending species, we additionally considered ants

as aphid mutualists in analysis. We observed no parasitized aphids (mummies) on trees. Hence, aphid parasitoids seemed not to play a role in aphid suppression in our study system early in the year. Densities of each herbivore or enemy group were summed over the two sampling months. Diversity of enemies was calculated as the number of different taxa (species, genera, or families, depending on the level of determination) per tree over the two sampling months.

LEAF HERBIVORY, INFECTION AND TREE GROWTH

Leaf herbivory was recorded on four trees per site in mid-June. We sub-divided each canopy into 8 sectors (bottom-top, right-left, and front-back). Then picked randomly (with closed eyes) from each sector one leaf of the interior (old wood) and one of the exterior (new wood) of the canopy, resulting in a stratified random sample of 16 leaves per tree. For each leaf, herbivory was estimated as percentage of leaf area lost by chewing insects in a scale of 0, 1, 2, 5, and then in increments of 5 % to a maximum of 100 % (Eichhorn et al. 2010, Lieurance and Cipollini 2012). In a pre-study, visual estimations were calibrated by comparing estimations with calculated values of scanned leaves in ImageJ 1.45s (Rasband 2012). Very young leaves (reddish or light greenish leaves) from the outermost 20 cm of new branches and leaves curled due to high aphid infestation were excluded. Damage to leaves by mining or scraping insects was also estimated but occurred only very occasionally (less than 0.05 % of total leaf area observed). Therefore, mining and scraping were not analysed. Fungal infection of leaves by shothole disease (*Wilsonomyces carpophilus*) was estimated in the same manner as leaf damage by herbivory. Tree growth was estimated per tree as increase in the length of all branches of the canopy between March and November 2012, divided by the length of all branches in March. This estimation results in a growth rate relative to tree size.

NUTRIENT AVAILABILITY, MICROCLIMATE AND GLUE RINGS

Vegetation mapping was conducted on the permanent grass strip below cherry trees (40 m² per study site), estimating the cover per plant species after Braun-Blanquet. Mean indicator values by Ellenberg (Ellenberg et al. 1992) for soil nitrogen (weighted by plant species cover) were calculated using the software Vegedaz (WSL 2012). Mean temperature and air humidity were measured approx. 1 m above ground at hourly intervals with data loggers (DS1923 Hygrochron iButtons, Maxim, Sunnyvale, USA). Chlorophyll content in leaves was measured 12 times per tree (two random twigs on the south and north side of trees, leaves no. 5 and 7 from top of each twig, and three repeated measurements per leaf and twig) with a chlorophyll meter (SPAD-502Plus, Konica Minolta Optics Inc., Tokyo, Japan). To separate the colonisation of trees by flying and walking arthropods, a glue ring (Raupen-Leimring, Neudorff GmbH; Emmerthal, Germany) was attached to three out of seven trees per site (Stutz and Entling 2011).

MIXED EFFECT MODELS

We performed Mixed Effect Models in R (R Development Core Team 2012) to test landscape effects on enemies, herbivores, and plant parameters. Response variables were calculated as mean values for trees with and without glue ring, and study site was included as a random term. Models were fitted by Laplace approximation with the function `glmer` in the R package `lme4` (Bates et al. 2012). According to Bolker (2009), we transformed the response variable where possible to obtain normality and homoscedasticity of residuals and used gaussian error distribution. If transformation was not successful, we used Generalised Linear Mixed Effect Models with poisson error distribution with rounded response variables (because poisson models demand integers). We added a random intercept term for each binomial count to model overdispersion (Warton and Hui 2011) if a model performed significantly better under the inclusion of the random term (based on model comparison with χ^2 -test). We removed outliers with Cooks' distances > 1 . The full models contained the following fixed factors: isolation from woody habitat, amount of woody habitat, and glue ring (to control for difference of arthropod communities between trees with and without glue ring). Models with density and richness of enemies and density of mutualistic ants as a response variable were computed with and without the corresponding resource density (herbivores as resource for enemies, aphids are resource for ants). For every response, the best-fitted model was selected according to Akaike's Information Criterion for small sample sizes (AICc) with dredge function in R package `MuMIn` version 1.7.7 (Barton 2012). Inference of single predictors in best models was assessed using χ^2 -tests comparing the maximum likelihood ratio between model with and without the respective variable (Bolker et al. 2009).

STRUCTURAL EQUATION MODELS

To test if herbivores were affected directly by the landscape or indirectly via enemy densities, we performed Structural Equation Models (SEM) in IBM SPSS AMOS Version 21. For SEM, observed arthropods were pooled per site, ignoring the differences between trees with and without glue ring. We first built sub models for aphids and herbivorous beetles, including as predictors all measures of enemy density and richness which were affected by landscape variables in Mixed Effect Models. We also included all landscape variables that predicted enemies or enemy richness, first as predictor of enemies, and second as direct effects on herbivores. We further added air temperature and humidity, nitrogen and chlorophyll values as predictors of herbivores. Best-fitted sub models according to AIC selection using the specification search function were then merged to an overall SEM including all landscape variables, nitrogen, chlorophyll, enemy densities and richness measures that remained in best-fitted sub models and predicted herbivores. Further, we included tree growth predicted by herbivore densities, leaf damage, and directly by landscape, climatic, nitrogen and chlorophyll values. Leaf infection was not included in the overall SEM because it was not affected by any landscape variable in Mixed Effect Models. The overall model was then simplified by AIC selection. In all

SEMs, densities were log- and rates logit-transformed (Warton and Hui 2011) where necessary to reduce skewness and excess of kurtosis in data.

Results

EFFECTS ON ENEMIES

Density of free-hunting spiders, density of spiders eating large prey and species richness of aphid and beetle enemies were lower on isolated cherry trees than on trees adjacent to forest or connected to other woody elements. In contrast, ladybeetles and hoverflies were more abundant at isolated sites compared to sites at the forest edges (Table 1). If resource density (aphids) was offered as predictor variable for those predators, the effect of habitat isolation became non-significant (Table 1). The amount of woody habitat in the landscape did not influence enemies. Five out of eight enemy groups and enemy richness of both aphids and herbivorous beetles were negatively affected by the presence of a glue ring (Table 1).

EFFECTS ON HERBIVORES AND MUTUALISTS

Aphids were only marginally (not significantly) reduced in landscapes with higher amount of woody habitat, but decreased with increasing richness of aphid enemies (Table 1 and Fig. 1). In addition, aphid densities increased with the chlorophyll content in leaves (Fig. 1) and decreased in presence of a glue ring (Table 1). Further, aphid density was positively correlated with densities of ladybeetles, hoverflies and ants. Aphid-mutualistic ants had higher densities at forest edges compared to isolated or connected sites, but only if aphid density was offered as predictor (Table 1). Herbivorous beetles showed higher densities on isolated trees (Table 1), but this effect was indirect via lower spider densities and richness of beetle enemies at isolated sites correlating negatively with beetle density (Fig. 1).

EFFECTS ON PLANT DAMAGE AND GROWTH

Leaf damage was only marginally affected by landscape factors (Table 1) but highly positively correlated with herbivorous beetle density and tree growth (Fig. 1). Tree growth was further negatively associated with aphid densities and positively with the availability of soil nitrogen (Fig. 1). Nitrogen had therefore on one hand a direct positive effect on tree growth and on the other hand an indirect negative effect mediated through higher chlorophyll content in leaves, correlating with higher aphid infestation damaging the tree. Leaf infection was not explained significantly by any landscape variables (Table 1).

Discussion

EFFECTS ON ENEMIES

Species richness of natural enemies, densities of free-hunting spiders and spiders eating large prey were negatively affected by habitat isolation. This indicates, as hypothesized, a reduced dispersal of enemies from woody habitats to isolated trees. In contrast, important aphid enemies (ladybeetles and hoverflies) were more abundant at isolated sites. However, this effect did not persist if density of aphids was included in the analysis because aphid densities positively influenced enemy densities (Table 1 and Fig. 1). These results strongly suggest that ladybeetles and hoverflies were bottom-up controlled by their prey rather than controlling it. A positive correlation between aphids and ladybeetles suggesting bottom-up effects on predators were also found in citrus groves (Piñol et al. 2009a). Modelling population growth of aphids in this system during the main spring peak revealed that the role of non-sedentary predators such as ladybeetles is secondary, as they track the aphids rather than controlling them (Piñol et al. 2009b). However, within predator groups the strength of bottom-up effects may differ between species (Sunderland and Vickerman 1980, Schellhorn and Andow 2005).

In our study, the amount of woody habitat in the landscape was not relevant for enemies (Table 1). This contradicts the general observation that density and richness of enemies is positively correlated with the amount of semi-natural habitat in agricultural landscapes (Bianchi et al. 2006, Tschardt et al. 2007, Chaplin-Kramer et al. 2011, Veres et al. 2013). Importantly, habitat amount and measures of fragmentation such as isolation are often correlated in landscapes (Fahrig 2003). Most of these studies do not take this into account, potentially misinterpreting observed landscape patterns (Lindenmayer and Fischer 2007). Alternatively, the relative importance of amount and isolation may differ between woody habitats studied in our system (stronger role of habitat isolation) and more dynamic annual crops and grasslands (stronger role of landscape composition), possibly due to higher mobility of organisms in disturbed herbaceous habitats (as shown for ballooning spiders in Entling et al. 2011).

EFFECTS ON HERBIVORES AND MUTUALISTS

Herbivorous beetles were positively affected by isolation from woody habitat. This effect was not direct but mediated through reduced enemy richness and density of spiders eating large prey at isolated sites. This indicates that herbivores were released from enemy suppression at isolated sites. In aphids, a similar pattern of enemy release was mediated through reduced enemy richness at isolated sites but did not lead to significantly higher aphid densities at isolated sites. This result contrasts the situation in the same study system three years earlier, where doubled aphid densities were found at isolated sites (Stutz and Entling 2011). Variation in herbivore densities between years may occur because of different weather conditions, namely temperature and rainfall affecting migration, reproduction and survival rates, and control by enemies (discussed in Thies et al. 2005). Alternatively, effects of isolation from other woody habitat on aphid densities may decrease with increasing age of trees.

Differences in aphid response to isolation between years underpin the importance of long-term experiments (Thies et al. 2005, Chaplin-Kramer et al. 2011).

Many different arthropod enemies colonised the cherry trees but only the density of spiders eating large prey negatively correlated with herbivores (Fig. 1). However, richness of enemies strongly negatively correlated with aphid and beetle densities (Fig. 1). In biological control, the release of multiple agents is mostly successful in controlling weeds, but generally not in controlling insect pests (Denoth et al. 2002). But control of herbivores by naturally occurring enemies in agricultural landscapes can be more effective if multiple enemies are present (Losey and Denno 1998, Snyder et al. 2006, Bael et al. 2008, Letourneau et al. 2009, Hogg et al. 2013). These emerging effects of multiple predators on prey can be additive or synergistic because different foraging strategies lead to complementarity in predation (Losey and Denno 1998, Sih et al. 1998). Alternatively, higher diversity increases the chance that a highly effective predator is present (Tilman et al. 1997, Loreau and Hector 2001, Straub and Snyder 2006, Philpott et al. 2009).

Densities of aphids and aphid-tending ants were positively correlated. Ants may have increased population growth of aphids by keeping natural enemies away from tree canopies (Styrsky and Eubanks 2007) or by reducing fungal infection risks through the removal of honeydew (Flatt and Weisser 2000). On trees with glue rings, where ants, most spiders, and earwigs were strongly reduced, aphid densities were considerably lower, indicating that direct benefits by ant-tending were more important than removal of enemies. Nevertheless, we cannot rule out that the positive correlation between ants and aphids partially occurred because ants were more active on trees with high aphid densities.

EFFECTS ON PLANT DAMAGE AND GROWTH

Plant damage and growth did not differ with isolation from or amount of woody habitat in the landscape. However, we detected enemies to be negatively correlated with habitat isolation, aphids to be negatively correlated with enemies, and tree growth to be negatively correlated with aphid densities (Fig. 1). This cascade suggests that negative effects of isolation on tree growth mediated through enemy diversity and aphid density may exist, especially because aphid densities and tree growth were positively affected by isolation in an earlier year (Stutz and Entling 2011). Aphids can develop large colonies in spring and early summer through asexual reproduction, causing leaf curling and growth reduction of developing shoots (McLaren and Fraser 2002). Nevertheless, a negative effect of aphids on plants is not trivial. In the presence of aphid-tending ants, many plants rather benefit from aphids because mutualistic ants remove a variety of other herbivores from trees (Styrsky and Eubanks 2007). Besides aphid density, nitrogen availability in the soil was an important factor for tree growth (Fig. 1). Therefore, tree growth was determined by a combination of bottom-up and top-down effects. Interestingly, leaf damage by herbivorous beetles was positively associated with tree growth. After being damaged by herbivores, about a third of studied plants species react with extensive growth

exactly compensating or even overcompensating the loss of tissue by herbivory (Hawkes and Jon 2001). Rapid plant regrowth is likely to have evolved as a strategy to reduce the negative impacts of damage (Belsky et al. 1993). However, overcompensating growth observed at the short term may not necessarily reflect long-term fitness benefits (Hawkes and Jon 2001). Alternatively, a positive correlation between beetles and plant growth may be explained by beetles favouring fast-growing trees. However, beetles were (in contrast to aphids) neither attracted by higher chlorophyll content of leaves nor by higher nutrient availability in the ground. This is in accordance with a general observation that sucking insects show a much stronger response to nitrogen availability than chewing insects (Butler et al. 2012).

Conclusions

In this study on multiple herbivores and multiple enemies on young cherry trees, isolation of cherry trees from the next woody habitat affected most enemies negatively but led to an increase in those enemies that are bottom-up controlled by herbivores. Herbivores themselves were positively affected by isolation or showed no response to it, partially supporting the hypothesis that herbivores are released from enemy suppression at isolated sites. The amount of woody habitat in the landscape, which was kept independent of isolation in our study, was not relevant for herbivore-enemy interactions. This highlights the importance to separate between effects of habitat amount and fragmentation. In contrast to our results, studies in annual crops often found strong effects of the amount of habitat in the landscape. This could be due to the lack of proper separation between habitat amount and isolation in earlier studies. Otherwise, it may mean that arboreal food webs respond differently to the landscape context than annual systems. We provide correlative evidence that enemy diversity is more important in controlling herbivores than the density of single enemy groups, supporting the hypothesis of additive or synergistic effects of multiple predators. Some mobile enemy groups, such as ladybeetles and hoverflies, were positively correlated with aphid density, suggesting that these enemies were bottom-up controlled rather than controlling their prey. Plant growth was affected to a similar degree by nutrient availability (bottom-up) and aphid density (top-down) but was not reduced by leaf damage of herbivorous beetles nor affected by landscape metrics. Altogether, the absence of landscape effects on plant growth, the differential effect of herbivore groups on plant growth, and the bottom-up control of some enemy groups by herbivores underline the need for studies including multiple enemies affecting multiple herbivores, crop damage, and plant growth. Differences in the response of aphids and tree growth to isolation between this study and observations three years earlier on the same trees suggest that fragmentation effects in perennial habitats change over time, and underpin the importance of long-term experiments.

Tables and Figures

Table 1. Enemy densities, richness, herbivore and mutualist densities, plant damage and growth of cherry trees in response to isolation of studied trees from other woody habitat, amount of woody habitat in the landscape, and density of prey for natural enemies. Shown are variables that remained in Linear Mixed Models after AICc model selection. Inference of single predictors was assessed using Chi²-tests, comparing the model with and without the respective variable. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ^t $p < 0.1$, ns $p > 0.1$.

| Response | Abbr. ¹ | Habitat isolation ² | | Habitat amount | | Glue ring | | Resource density | | | Dev. ³ | E.d. ⁴ |
|-----------------------------------|--------------------|--------------------------------|------------------|----------------|-------------------|-----------|-------------------|------------------|-------|----------|-------------------|-------------------|
| | | Est. | Chi p | Est. | Chi p | Est. | Chi p | Type | Est. | Chi p | | |
| Natural enemy densities | | | | | | | | | | | | |
| Ladybeetles | CO | | | | | | | Aphids | 0.004 | 17.2 *** | 12% | qp |
| Ladybeetles ⁵ | CO | (a+c)<i | 5.5 ^t | | | | | | | | 4% | qp |
| Hoverflies | SY | | | | | | | Aphids | 0.003 | 14.3 *** | 27% | p |
| Hoverflies ⁵ | SY | a<i | 7.6 * | | | -0.92 | 2.7 ^{ns} | | | | 19% | p |
| Earwigs | EA | | | | | -1.59 | 35.6 *** | | | | 18% | qp |
| Spiders (net) | SN | | | | | | | | | | 0% | gs |
| Spiders (free) | SF | (a+c)>i | 15.7 *** | | | -0.36 | 10.6 ** | | | | 27% | gs |
| Cantharidae | CA | | | | | | | Beetles | 0.07 | 5.0 * | 17% | p |
| Cantharidae ⁵ | CA | | | | | | | | | | 0% | p |
| Spiders (large) | SL | a>c>i | 11.4 ** | | | -0.26 | 7.8 ** | | | | 14% | gs |
| Natural enemy richness | | | | | | | | | | | | |
| Aphid enemies | RA | a>i | 13.2 ** | | | -0.70 | 12.6 *** | | | | 15% | g |
| Beetle enemies | RB | a>(c+i) | 18.0 *** | | | -0.23 | 5.3 * | | | | 27% | g |
| Herbivore and mutualist densities | | | | | | | | | | | | |
| Aphids | AP | | | -0.02 | 2.4 ^{ns} | -2.14 | 10.9 *** | | | | 5% | gl |
| Herb. beetles | PH | a<(c+i) | 6.4 * | | | | | | | | 6% | gl |
| Ants | AN | a>(i+c) | 6.8 * | | | -0.89 | 20.0 *** | Aphids | 0.001 | 18.4 *** | 30% | gl |
| Ants ⁵ | AN | | | | | -1.19 | 29.8 *** | | | | 17% | gl |
| Plant damage and growth | | | | | | | | | | | | |
| Leaf damage | LD | a<i | 5.3 ^t | | | | | | | | 5% | glt |
| Leaf infection | IN | | | | | | | | | | 0% | glt |
| Tree growth | TG | | | | | 0.07 | 2.5 ^{ns} | | | | 25% | gs |

¹ Abbreviations for response variables used in Fig 1.

² Levels of habitat isolation: a = adjacent to forest, c = 100 – 200 m away from next forest edge but connected to small scale woody habitats (single trees, hedgerows, orchards), i = isolated from any woody habitat by 100 – 200 m.

³ Percentage of the total residual deviance that is explained by the model.

⁴ Type of error distribution and transformation of response variable: g = gaussian distribution, gl = gaussian distribution with log transformed response, glt = gaussian distribution with logit transformation, gs = gaussian distribution with square root transformed response, p = poisson distribution, qp = quasi-poisson distribution (with inclusion of a random observation term; see Material and Methods for details).

⁵ Model selection performed without providing resource density in full model.

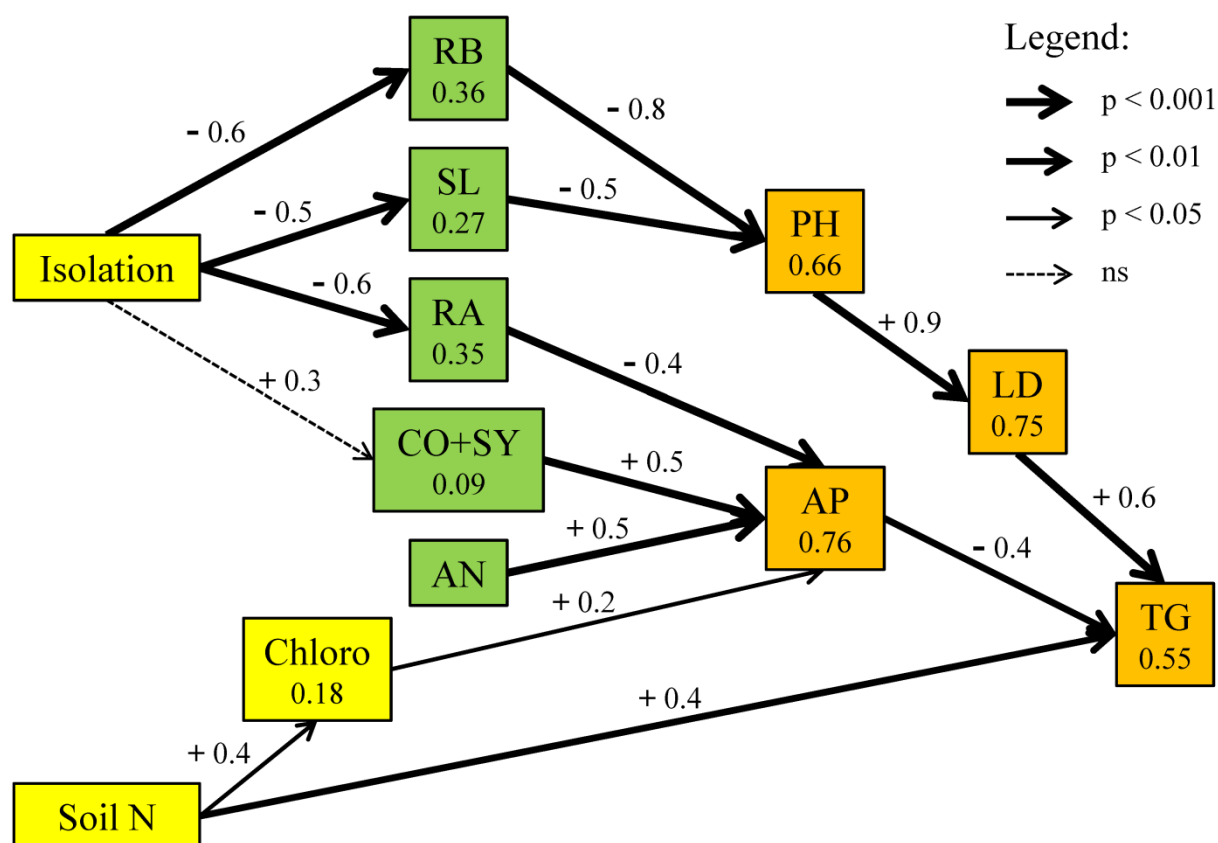


Figure 1. Final Structural Equation Model showing relationships between isolation from woody habitat (Isolation), soil nitrogen availability (Soil N), chlorophyll content of leaves (Chloro), densities and richness of natural enemies (RB, SL, RA, CO, SY and AN), densities of herbivores (PH and AP), leaf damage (LD), and tree growth (TG). Abbreviations for enemy and herbivore groups are explained in Table 1. Relationships are indicated with standardised regression weights (slope of relationship between standardised predictor and response) and size of arrows indicates p-values for regression (probability that a slope is equal to zero). Explained variation of response variables (sum of squared standardised regression weights) is indicated within the boxes.

General Discussion and Outlook

Effects of disturbance on biodiversity

Human disturbance of natural habitat through intensive farming is generally considered as detrimental to biodiversity (Tilman 1999, Kremen et al. 2002, Tscharntke et al. 2005, Chacoff and Aizen 2006, Tscharntke et al. 2012). In contrast, disturbance through environmental-friendly farming is predicted to have a lower impact or even benefit biodiversity (Connell 1978, Perfecto and Vandermeer 2010, Tscharntke et al. 2012). I showed that disturbance of tropical forest by agricultural activities can increase alpha and beta diversity of bees and wasps (Chapter 1). These positive effects of disturbance might have three reasons: First, the investigated system was disturbed only at a small scale while protected forest surrounded agricultural areas. Second, disturbance was kept at a low level in the sense that some vegetation structure of the natural forest remained in agricultural areas and pesticide and fertiliser input was moderate. Third, agricultural practices were diverse and led to a heterogeneous landscape. Low input and heterogeneous agricultural landscapes similarly increased local biodiversity in Europe, compared to fully natural landscapes before agricultural expansion (Stoate et al. 2001, Blondel 2006, Zeder 2008, Colombaroli et al. 2013; but see Navarro and Pereira 2012). Of course, nowadays natural and undisturbed habitat is very important for biodiversity conservation in the tropics (Barlow et al. 2007, Laurance et al. 2012). Therefore, it would be wrong to conclude that conversion of tropical forest into heterogeneous, small-scale farming systems is desirable for biodiversity conservation. But taking into account the increased competition for land (Godfray et al. 2010), it may be tolerated from the perspective of bee and wasp conservation. However, bees and wasps might be less disturbance-sensitive than other taxa (Barlow et al. 2007) and cross-taxon congruency in responses of biodiversity to disturbance is generally low (Barlow et al. 2007, Dormann et al. 2007, Gardner et al. 2009, Kessler et al. 2009, Axmacher et al. 2011). Therefore, disturbance effects on bees and wasps cannot be extrapolated to overall biodiversity.

In my research in Belize, I sampled bees and wasps with traps in forest and agricultural areas, measuring the activity of species rather than their actual fitness. It remained unclear, whether surrounding forest was a vital component within the life cycle of some or many of the species collected in farmland and whether forest served as a source for colonisation of agricultural areas (Chapter 1). Therefore, future ecological research should measure the contribution of different habitat types to reproductive success of species (discussed in Kleijn et al. 2011). Additionally, integrating the socio-economic aspects of agricultural systems is important for research on habitat disturbance in the tropics (Perfecto et al. 2009). For example, probable future intensification given the actual socio-economic conditions of the farmers should be considered, as well as potential negative effects of biodiversity reserves for local communities. Separating people from resources can lead to high pressures on reserves through illegal activities and therefore reduce the effectiveness of protected areas in biodiversity conservation (Perfecto et al. 2009, Laurance et al. 2012).

Taxonomy and biology of arthropods

Comprehensive comparisons of the conservation value (Gardner et al. 2009) of different species in disturbed and undisturbed forest were not possible in Belize. Sound information on species distributions, rarity, and specialisation was missing (Chapter 1). Furthermore, some individuals could only be determined to morphospecies because taxonomy of arthropods is often poor in the tropics. In many countries, invertebrates (or flora and fauna in general) are not sufficiently sampled (see example in Chapter 2). Missing knowledge on taxonomy and biology of species limits the value and potential application of ecological studies (Swiss Academy of Sciences 2007, Smith et al. 2011, Bacher 2012). On the other hand, ecological studies on arthropods in the tropics contribute to the knowledge on the biology of involved species (Chapter 1) and provide a source of valuable material for taxonomic research (Chapter 2).

The landscape scale

Knowledge about effects of the amount of semi-natural habitats in the landscape and isolation from those habitats is essential for biodiversity conservation in agricultural landscapes (Tscharntke et al. 2005, Tscharntke et al. 2012). In my research, the amount of woody habitat affected biodiversity of insects visiting cherry flowers (Chapter 3) and isolation from the next woody habitat affected herbivores and their natural enemies in the canopy of cherry trees (Chapter 5). The presence of landscape effects on biodiversity is in accordance with both ecological theory (Bengtsson 2010) and management recommendations (Tscharntke et al. 2005, Kremen et al. 2007). Experimentally created study sites with standardised local conditions (as used in Chapters 3 and 5) are a powerful tool to study the impacts of different landscape factors on biodiversity. However, standardisation of local factors remove differences in resources or structure between patches and hence differences in biodiversity (see 'species sorting' in Bengtsson 2010). Therefore, standardising local settings does not allow comparison of the relative importance of local and landscape effects. Furthermore, some research questions about the mechanisms underlying observed patterns are difficult to assess in studies on the landscape scale. For example, pollination success can be increased by higher abundance and/or richness of pollinators but both measures are often correlated in natural communities (Chapters 1, 3 and 4). To fully understand the relative importance of abundance versus richness for ecosystem functions, manipulative experiments are necessary (Albrecht et al. 2012). However, they are difficult to perform under realistic scenarios, for example including entire communities occurring in real ecosystems. Landscape studies can at least reveal correlative evidence for mechanism (Lindenmayer and Fischer 2007, Coudrain et al. 2013).

When designing landscape experiments, land cover types are often divided into 'habitat' and 'matrix'. In agricultural settings, the matrix is often of lower but still of some value to biodiversity (Bengtsson 2010, Tscharntke et al. 2012). Classifying the landscape into dichotomous descriptors may not reflect the functionality of cover types for biodiversity (discussed in Veres et al. 2013). Therefore, landscape

effects in agricultural landscapes may be different than expected by the island biogeography theory (discussed in Kremen et al. 2007, Bengtsson 2010). ‘Habitat’ should refer to the resources and conditions that produce occupancy for species (Hall et al. 1997). Using functional landscape metrics is one possibility to include the value of each cover type for biodiversity (Fahrig et al. 2011, Mühlner et al. 2012) but this method relies on often subjecting estimation of habitat values for species and needs to be adapted for each investigated species. Future research, for both ecological theory and applied science, should adequately define the value of the agricultural matrix for the survival or dispersal of species (Lindenmayer and Fischer 2007, Bengtsson 2010).

Habitat loss versus fragmentation

The separation of habitat amount, as a spatial substitute for habitat loss over time, and habitat isolation, as a measure of fragmentation, proved to be useful in understanding landscape effects on biodiversity and ecosystem functions. The amount of woody habitat, but not isolation, increased insect visitation rates to cherry flowers (Chapter 3). In contrast, isolation, but not habitat amount, affected herbivore-enemy interactions on cherry trees (Chapter 5). Importantly, habitat amount and measures of fragmentation such as isolation are often correlated in landscapes (Fahrig 2003). Studies on pest control generally observe that density and richness of enemies are positively correlated with the amount of semi-natural habitat in agricultural landscapes (Bianchi et al. 2006, Tschardt et al. 2007, Chaplin-Kramer et al. 2011, Veres et al. 2013). But most studies do not take into account the correlation of landscape variables, potentially misinterpreting observed landscape patterns. To successfully design and manage agricultural landscapes that maintain biodiversity and ecosystem services, experimental evidence for effects of both habitat loss and fragmentation is needed (Kremen 2005, Kremen et al. 2007, Tschardt et al. 2007, Hadley and Betts 2012, Tschardt et al. 2012). Our results support the theoretical prediction that biodiversity can be increased by maintaining both connectivity between patches and complex landscapes with a high share of semi-natural landscapes (Bengtsson 2010, Tschardt et al. 2012).

Provider-centred versus function-centred approach

Organisms involved in ecosystem functions (providers) differ in their effectiveness with which they fulfil their ecological functions (Kremen 2005). Therefore, landscape effects on ecosystem functions may not be well predicted from effects on their providers. The abundance of pollinators on cherry trees was affected by the amount of woody habitat, but the associated pollination function was not (Chapter 3). In contrast, the density of herbivorous beetles and their damage to cherry leaves were both affected by habitat isolation (Chapter 5). Therefore, it was important to differentiate between provider and function to understand the delivery of pollination but it did not improve the understanding on beetles and their damage. The difference between the two systems (pollinators and beetles) can be explained as follows: The presence of pollinators alone is not sufficient to provide the pollination function. In

many plants, pollinators need to carry a high share of compatible pollen from other individuals of the same plant species to successfully pollinate flowers (Wilcock and Neiland 2002). Therefore, pollination success depended on the proximity to pollen sources rather than the amount of woody habitat (Chapter 3). In contrast, herbivorous beetles do not require additional resources in order to damage plants. On cherry trees, ladybeetles and hoverflies were bottom-up controlled by aphids rather than suppressing them, resulting in a positive rather than negative relationship between aphids and enemies (Chapter 5). In this case, assessing natural enemies (providers) does not inform about aphid suppression (function provided by enemies) and effects of enemies on herbivores need to be assessed properly in cage experiments excluding enemies (Chaplin-Kramer et al. 2011, Chaplin-Kramer and Kremen 2012). Further, I found correlative evidence that overall enemy diversity rather than abundance of single groups was important in controlling aphids, suggesting that multiple enemies are more effective in suppressing herbivores (Chapter 5, but see comments on separating richness and abundance effects in the previous section ‘The landscape scale’). Such diversity effects can arise because of different foraging strategies leading to complementarity in predation (Sih et al. 1998) or because higher diversity increases the chance that a highly effective predator is present (Tilman et al. 1997, Loreau and Hector 2001, Straub and Snyder 2006, Philpott et al. 2009).

Applied research on ecosystem services

I found direct effects of habitat amount or isolation on beneficial arthropods (providers) in both plant-pollinator (Chapter 3) and plant-herbivore-enemy interactions (Chapter 5). In contrast, the associated services, fruit set and plant growth, were only partly affected by the landscape. In general, discrepancy between responses of natural enemies and plant growth may have several reasons: First, not only natural enemies but also herbivores may be affected positively by complex landscapes (Roschewitz et al. 2005, Martin et al. 2013) or connectance to semi-natural habitat (Landis et al. 2000). Second, negative interactions between simultaneously enhanced enemies may constrain pest control (Martin et al. 2013). Third, enemies may attack pests but also damage plants (Suckling et al. 2006, Eilers and Klein 2009). In order to successfully apply ecological research in the management of agricultural areas, ecologists urgently need to consider potential negative effects associated with semi-natural habitat in agricultural landscapes.

The practical application of ecological research in biodiversity conservation can only take place if variables measured by scientists are simple and applicable (discussed in Fahrig et al. 2011). For example, isolation of fields from woody habitat can be reduced relatively easily by planting hedgerows. In contrast, the amount of forest in agricultural landscapes is more difficult to extend dramatically without compromising the farmland needed for production. The compatibility of implemented schemes with farmers’ values, such as productivity, is essential for successful restoration of agricultural landscapes (Burton et al. 2008). Academics reduce the complexity of a system to a few isolated research parameters, while practitioners are facing the reality of a complex system (Braunisch

et al. 2012). For example, there is strong scientific evidence that increased biodiversity generally leads to increased functioning of ecosystems (Cardinale et al. 2012). However, this knowledge mostly comes from controlled experiments rather than from real landscape studies conducted at a scale relevant for management (but see Gamfeldt et al. 2013). Despite these caveats, new solutions to bring together scientific research and landscape management are emerging: Scientists need to investigate effects generated by the implementation of environmental schemes (e.g. Aviron et al. 2009) or implement landscape changes themselves, preferably in collaboration with practitioners. Under this scenario, the applicability of measured variables is given and scientific results are likely to hold in natural system because hypotheses are tested in real scenarios.

Knowledge exists about how biodiversity is affected by the landscape (Tscharntke et al. 2012) and how diversity affects ecosystem functions (Cardinale et al. 2012), but methods that maintain or increase biodiversity in order to actually enhance ecosystem services are less developed (discussed in Chapter 4) and should be a focus of future research. To overcome opposition of some farmers to implement environmental schemes (e.g. Burton et al. 2008), it can be useful to simultaneously investigate multiple services gained by those schemes (Wratten et al. 2012, Gamfeldt et al. 2013) but openly address also possible adverse effects and trade-offs between services. Further, ecosystem services such as pollination might be best obtained by combining natural and managed providers (e.g. wild pollinators and honeybees), to increase efficiency and reduce risks associated with the dependency on a single strategy (Chapter 4).

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LeiterIn der Arbeit: Prof. Dr. Martin H. Entling

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Ben, 15.2.2013

Ort/Datum

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