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Insect and mollusc communities in wildflower strips: Effects of plant diversity and surrounding landscape in an agro-ecosystem

THESIS

presented to the Faculty of Science of the University of Fribourg (Switzerland)
in consideration for the award of the academic grade of
Doctor rerum naturalium

by

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Dissertation Nr. 1780
UniPrint
2013

Accepted by the Faculty of Science of the University of Fribourg (Switzerland) upon the

recommendation of Prof. Dr. Owen Petchey, and Prof. Dr. Christian Lexer.

Fribourg, 25.01.2013 (date of oral examination)

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Für Ronja und Malyn.

„*Ich habe keine besondere Begabung, ich bin nur leidenschaftlich neugierig.*“

Albert Einstein (1879-1955)

„Wir sind nicht nur für das verantwortlich was wir tun, sondern auch für das was wir nicht tun.“

Molière (1622-1673)

„*Gehe nicht, wohin der Weg dich führen mag, sondern dorthin wo kein Weg ist und hinterlasse eine Spur.*“

Jean Paul (1763-1825)

Contents

SUMMARY

Agricultural land covers approximately 38% of the world's land area, so its contribution to biodiversity is critical for successful conservation in the future. Managed in the right way, agriculture can contribute to the conservation of high-diversity systems, which may provide important ecosystem services such as pollination and biological control. The identification of environmental factors that structure biodiversity is central to the assessment of the impact of land use and climate changes and the planning of conservation strategies. The quality, proportion and spatial arrangement of semi-natural habitats and overall habitat heterogeneity in intensively-used agricultural landscapes are thought to play major roles. Aiming to better understand community organization in spatially-structured ecosystems, we made use of sown wildflower strips. Over the last decade, these ecological compensation zones have been established in the matrix of our intensive agriculture to conserve biodiversity. We conducted a semi-natural experiment in wildflower strips, manipulating trophic structure (reduction of herbivorous molluscs and of major predators) and plant diversity (2, 6, 12, 20 and 24 sown species) to assess the effect of plant diversity, biomass and composition on different functional groups of invertebrates that are of specific importance for agriculture.

First we experimentally assessed the effect of plant diversity, biomass and composition on molluscs, and *vice versa*, the effect of mollusc abundance on vegetation. We showed that plant diversity, structure and composition can have substantial effects on mollusc abundance and composition. The agricultural pest species *Arion lusitanicus* was less abundant in more diverse habitats. Species rich communities thus appear to be more resistant against generalist herbivores. Plant species composition was the most important determinant of the gastropod community. Thus selective feeding and active habitat choice in molluscs might be the reason for lower abundances in diverse habitat patches. An optimization of the species composition of wildflower strips could thus reduce their attractiveness to slugs. We also provide evidence for a significant decrease in plant species richness caused by molluscs after three years of the experiment, resulting in a compositional change of the vegetation. Our results demonstrate the protective role of plant biodiversity against generalist herbivores, which would otherwise negatively impact plant diversity on a longer term, driving the system along a "low plant diversity – high mollusc abundance" trajectory.

Second, we focused on hymenopteran-based food webs in standardized trap nests that allowed us to study species richness, abundance, and quantitative interactions of above-ground nesting bees and wasps that act as pollinators and biological control agents, and their natural enemies. We simultaneously analyzed the effects of plant species richness, vegetation structure and plant composition on these trap-nesting communities at a small spatial scale. Decreasing plant species richness resulted in lower wasp species richness and fewer brood cells of spider-predating wasps. However, for some functional groups, namely bees, aphid- and herbivore-predating wasps, we found no effects of vegetation. Spider abundances in the wildflower strips were regulated by top-down and bottom-up control by spider-predating wasps and herbivores, respectively. Our results indicate that plant diversity loss has strong effects on mobile hymenopterans that are limited by the load of their prey. We conclude that preserving even small biodiversity hotspots with a particular rich plant composition can benefit the conservation of biodiversity in agricultural landscapes.

Third, we assessed the diversity and abundance of the trap-nesting communities at the landscape scale, and compared the importance of landscape composition and heterogeneity, of spatial arrangement, and of vegetation diversity, composition and structure on the complexity and the organisation of the hymenopteran food web. The proportion of forest cover close to wildflower strips stood out as the most influential landscape element, resulting in a richer trap nest community with more links between species in the food webs and a higher diversity of interactions. Forest close to wildflower strips increased the quantitative food-web metrics vulnerability and generality, while plant species richness was positively related to compartmentalization.

Our study revealed the necessity to restore a dense network of flower-rich habitat patches in agricultural landscapes and also to conserve a diverse landscape mosaic with high proportions of woody habitat, in order to 1) ensure long-term sustainability of ecosystem services such as pollination and biological control, and 2) attract fewer, and maintain a low impact of potentially problematic herbivores.

ZUSAMMENFASSUNG

Fast 38% der Landfläche unserer Erde wird landwirtschaftlich genutzt. Ihr Beitrag zur Biodiversität ist deshalb wichtig für den Umweltschutz. Wenn landwirtschaftliche Flächen nachhaltig genutzt werden, können sie zu einer hohen Diversität beitragen, was sich positiv auf sogenannte Ökosystemleistungen wie Bestäubung und biologische Schädlingsbekämpfung auswirkt. Die Identifizierung von Umweltfaktoren, welche die Biodiversität erhöhen, ist wichtig für die Einschätzung des Einflusses der Landnutzung und der Planung von Umweltschutzstrategien. Die Qualität, Fläche, räumliche Verteilung und Heterogenität von naturnahen Habitaten spielen eine wichtige Rolle in intensiv genutzter landwirtschaftlicher Fläche.

Mit dem Ziel Lebensgemeinschaften in räumlich-strukturierten Ökosystemen besser zu verstehen und damit schützen zu können, führten wir eine Studie in Buntbrachen durch. Im letzten Jahrzehnt wurden diese ökologischen Ausgleichsflächen innerhalb von landwirtschaftlichen Flächen etabliert, um die Biodiversität zu erhöhen. Für unsere Studien etablierten wir 12 Buntbrachen in intensiv genutzter Landwirtschaft und manipulierten die Abundanz von Herbivoren (Schnecken und Kleinsäugern) und ihren natürlich vorkommenden Feinden (Igeln, Raubvögel und Füchsen), sowie die Artenvielfalt von Pflanzen (2, 6, 12, 20 und 24 gesäte Arten). Somit konnte der Effekt der Vegetation auf verschiedene landwirtschaftlich relevante Invertebraten Gruppen gemessen werden.

Im ersten Experiment untersuchten wir den Effekt der Pflanzenmischung, Diversität und Struktur auf Schnecken, und *vice versa*, den Effekt der Schnecken auf die Vegetation. Unsere Ergebnisse zeigten, dass alle drei Vegetationsmerkmale einen wesentlichen Einfluss auf die Schneckenanzahl und Zusammensetzung haben. Vor allem die Art, die den grössten landwirtschaftlichen Schaden hervorruft, *Arion lusitanicus*, die Spanische Wegschnecke war

viel weniger häufig in einem Habitat mit hohem Pflanzenartenreichtum. Wir schliessen daraus, dass artenreiche Flächen resistenter gegen generalistische Pflanzenfresser sind. Die Artenzusammensetzung der Pflanzen hatte bei weitem, den größten Einfluss auf die Schneckengemeinschaft. Der selektive Fraß und aktive Habitatswahl sind Gründe für eine geringere Anzahl an Schnecken in artenreichen Flächen. Eine Optimierung der Pflanzenartenmischung in Buntbrachen könnte somit ihre Attraktivität für Schnecken reduzieren. Der Pflanzenartenreichtum wurde drastisch durch den Schneckenfraß reduziert, was zu einer Veränderung der Pflanzenmischung führte. Unsere Ergebnisse zeigten somit eine Schutzfunktion der Pflanzendiversität gegen generalistische Herbivoren, welche wiederum einen negativen Einfluss auf die Pflanzendiversität haben können, was längerfristig zu „niedriger Pflanzendiversität bei hoher Herbivorenzahl“ führen könnte.

Im zweiten Experiment analysieren wir Gemeinschaften und Nahrungsnetzte basierend auf solitären Bienen und Wespen in standardisierten Nisthilfen. Diese ermöglichten uns den Artenreichtum und die Abundanz dieser Bestäuber, und natürlichen Feinden von landwirtschaftlichen Schädlingen, ihren eigenen Feinden und ihrer Beute zu bestimmen. In unserer ersten Studie an diesem System untersuchten wir klein-räumliche Effekte der Pflanzenmischung, Diversität und Struktur auf diese Lebensgemeinschaften. Unsere Ergebnisse zeigten einen starken Rückgang der Wespendiversität mit sinkendem Pflanzenartenreichtum und eine geringere Abundanz an spinnenfressenden Wespen. Für andere trophische Gruppen, wie bienen- und herbivorenfressenden Wespen fanden wir entgegen unserer Erwartung keinen Einfluss. Desweiteren zeigte sich, dass die Spinnengesellschaft wahrscheinlich durch die spinnenfressenden Wespen von oben und gleichzeitig durch die Abundanz ihrer Beute von unten reguliert wird. Anhand unserer Studie konnten wir zeigen, dass ein Pflanzenartenrückgang einen Einfluss auf mobile Insekten haben kann, wenn diese stark von Grösse und Gewicht ihrer Beutetiere limitiert werden. Wir schlussfolgern, dass die Etablierung und Erhaltung von selbst kleinen Biodiversitäts-„Hotspots“ in der Landwirtschaft von grossem ökologischem Nutzen sein kann.

Im dritten Experiment untersuchten wir wieder die Diversität und Abundanz der Bienen- und Wespengemeinschaften, aber diesmal auf der Landschaftsebene. Hierzu studierten wir den Einfluss der Landschaftszusammensetzung, der räumlichen Verteilung der Buntbrachen und der Vegetation auf die Artenzusammensetzung in Nisthilfen und die Struktur der Nahrungsnetze. Waldflächen in der Nähe von Buntbrachen hatten den stärksten Einfluss, was sich in einem größeren Artenreichtum der Nisthilfenbewohner und einer größeren Diversität an Interaktionen wiederspiegelte. Waldflächen in der Umgebung von Buntbrachen beeinflussten auch die quantitativen Messwerte und die Struktur der Nahrungsnetze, was theoretisch zu einer höheren Stabilität der Gemeinschaften führt.

Unsere Studie zeigte, dass in intensiv genutzter Agrarlandschaft ein dichtes Netz von artenreichen Ausgleichsflächen mit einem hohen Anteil an Waldflächen wichtig ist, um 1) Ökosystemleistungen wie Bestäubung und biologische Schädlingsbekämpfung langfristig zu erhalten, sowie 2) die Anzahl und den Einfluss von problematischen Herbivoren zu reduzieren.

GENERAL INTRODUCTION

Rapid population growth and the industrial revolution have led to dramatic changes in global land use over the last two centuries, with approximately 38% of the planets terrestrial ground being agricultural area (Figure 1; Watson *et al.* 2004; World Bank Institute 2012). Land use intensification has been identified as one of the greatest threats for biodiversity, beside climate change (Kleijn *et al.* 2009). Biodiversity includes the richness (number), eveness (equity of relative abundance), and composition (types) of alleles, species, functional groups, or ecosystems (Isbell 2012). Ecosystem functioning (e.g. productivity, nutrient cycling) and ecosystem stability (i.e. temporal invariability of productivity) depend on biodiversity (Naeem *et al.* 1999; Loreau *et al.* 2001). Its loss may diminish human well-being by decreasing the services that ecosystems can provide for people (Balvanera *et al.* 2006). In some cases, human actions have promoted biodiversity. Conservation strategies, such as creating parks or restoring ecosystems, allow the protection of biodiversity and ecosystem functioning, with a great potential of benefits especially in agricultural ecosystems (Benayas & Bullock 2012). Thus, investigations must focus on the optimization of conservation and restoration strategies.

Source: Millennium Ecosystem Assessment 2005

Figure 1. Approximately 38% of the earth’s terrestrial surface is occupied by agricultural area.

To better understand the causes and consequences of species declines, biodiversity experiments have been conducted, usually in grasslands, e.g. *Cedar Creek* (Tilman *et al.* 1997a), *Biodepth* (Hector *et al.* 1999), *Jena experiment* (Roscher *et al.* 2004). Much of this work discussed the impact of plant species loss on the stability of ecosystems (MacArthur & Wilson 1967; Loreau *et al.* 2001; Tilman *et al.* 2001; Haddad *et al.* 2011; Cardinale *et al.* 2012) and numerous studies showed that an increase in plant species richness results in better resource use and thus enhances ecosystem functioning in terms of productivity. Two underlying mechanisms have been identified: the complementarity and sampling effect (MacArthur & Wilson 1967; Loreau *et al.* 2001; Tilman *et al.* 2001; Haddad *et al.* 2011; Cardinale *et al.* 2012). The sampling effect refers to the increased probability of a highly productive or competitive species being present at high diversity levels (Huston 1997). In contrast, complementarity of species is considered to be the result of niche partitioning and facilitation, by which certain species modify environmental conditions in a way that promotes the performance of other co-occurring species. This results in increased performance of the community when compared to that of single species (Loreau 2000).

These studies showed that ecosystem functioning often depends on species richness, composition, and functional group richness, and can also depend on species evenness and genetic diversity (Tilman *et al.* 1997a; Tscharntke *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Tylianakis *et al.* 2006). However, the relationship between diversity and ecosystem functioning is not that straightforward when trophic and spatial aspects are taken into account. Theoretical work suggests that the results of diversity experiments in plant communities may be complicated when higher trophic levels are included in the system (Thebault & Loreau 2003; Duffy *et al.* 2007; Thebault *et al.* 2007; Haddad *et al.* 2009).

Herbivores, for example, can affect plant diversity and community composition by selectively feeding upon particular species and altering competitive interactions (Buckland &

Grime 2000; Buschmann *et al.* 2005; Howe *et al.* 2006; Scherber *et al.* 2010b; Allan & Crawley 2011). Herbivory can affect plant diversity positively, negatively, or neutrally, depending on the herbivore species and habitat type. Abundances of herbivores might be related to plant diversity. Two contrasting hypotheses focusing on plant-herbivore interactions have been formulated. The *more individuals hypothesis* (Srivastava & Lawton 1998) suggests that diverse plant communities are often more productive than simple plant communities (Tilman *et al.* 2001) and provide a greater quantity of resources for consumers, thereby increasing their number. Further, herbivores may also increase their consumption and biomass when feeding on a more diverse plant community, as is the case in grasshoppers (Pfisterer *et al.* 2003; Unsicker *et al.* 2008). While the *more individuals hypothesis* assumes a similar effect on all herbivore species, the *resource concentration hypothesis* (Root 1973) makes a prediction only for specialist herbivores: specialist populations are expected to increase when their food plants are at high abundance. Therefore, species-poor plant communities should show higher specialist herbivore abundances than diverse plant communities where host plants are more dispersed. The situation is less clear for generalists, although they can also show feeding preferences (Scherber *et al.* 2010b) and thus should respond to changes in plant composition. Thus, in **Chapter 2** we focus on the abundance of generalist herbivores (molluscs) in a gradient of plant diversity.

Another important focus in biodiversity research is the conservation of a high diversity of mutualistic and antagonistic interactions, which has been identified to be of great importance (e.g. Thebault & Loreau 2006; Tylianakis, Tscharntke & Lewis 2007; Ings *et al.* 2009), especially as ecosystem services associated with species interactions such as pollination and biological control are of particular interest for human welfare (Balvanera *et al.* 2006; Cardinale *et al.* 2012). Food-web structure received particular attention in theoretical models aiming to predict the effect of structural food-web complexity on the dynamics and stability of communities (MacArthur 1955; May 1972; McCann 2000). Recent studies focused on the effects of habitat change on food-web structure in insect communities, and predicted that changes in food-web structure can occur even faster than simple species richness, in response to habitat declines (e.g. Albrecht *et al.* 2007; Tylianakis *et al.* 2008; Gagic *et al.* 2011). Some studies however, did not support this finding (Kaartinen & Roslin 2011). Thus, the effects of plant diversity loss and landsape composition on detailed quantitative food webs remain still unclear (but see Haddad *et al.* 2009). In **Chapters 3** and **4** we thus investigate detailed quantitative food webs of cavity-nesting bees, wasps and their enemies in trap nests. Here we focus on the diversity and abundance of the whole communities, with special regard to the diversity and abundance of functional trophic groups and the quantitative food-web structure of these communities.

The classical biodiversity experiments give detailed and specific insights into causes and consequences of local diversity loss on a small scale; however, investigation at larger spatiotemporal scales in managed ecosystems would further improve our understanding of the consequences of biodiversity declines. Thus our experiment is situated in an agricultural landscape.

WILDFLOWER STRIPS - ONE FORM OF AGRICULTURAL COMPENSATION ZONE

Agricultural land use and biodiversity conservation have been traditionally viewed as incompatible. Crop fields mainly used for cereal production have expanded at the cost of non-crop areas, and hedges and fallow strips have been lost in the course of field enlargement (Stoate *et al.* 2001). To counter species decline, agri-environmental schemes were introduced in Europe. These are payments to farmers and other landholders to address environmental problems or to promote the provision of environmental amenities (OECD 2003). The most important measure within the Swiss agri-environmental scheme is that at least 7% of farmland must be managed as ecological compensation areas. These include a wide variety of specific biotopes such as orchards, hedges, extensively managed hay meadows or wildflower strips. These areas are ideally arranged as part of a network in the landscape (Haaland & Gyllin 2011), with farmers receiving greater subsidies if their ecological compensation areas are part of a designed network. The geographical arrangement of the elements within these networks and the effect on different functional groups have, however, rarely been studied.

Sown wildflower strips are a rather new landscape element functioning as an ecological compensation area in Central and Northern Europe (Haaland *et al.* 2011). They are usually sown with seed mixtures of 24 wild flowers (Figure 2) on arable land and along field boundaries and are kept and subsidized for six years. At that time succession has often gone so far that the strips are dominated by grass, bushes and trees. Winter mowing is recommended to farmers on a voluntary basis, but in many cases there is no form of management besides spot-treatment of certain weed species (Haaland *et al.* 2011).

In addition to enhancing biodiversity in the agricultural landscape, crucial aims for establishing wildflower strips are to ensure crop pollination by wild pollinators and to ensure biological pest control by favouring predators (Nentwig 2000). Thus one focus of wildflower management is on enhancing wild bee and wasp communities.

Wildflower strips are also favourable habitats for herbivores, such as aphids, molluscs (Günter 2000; Frank 2003) and rodents (Aschwanden *et al.* 2007), that have the potential to harm agricultural crops. The strips may provide additional resources and dense cover in agricultural landscapes, because several of the plant species included in the mixture are eaten by problematic herbivores and also offer reproduction sites and protection (Briner & Frank 1998).

In our study, we conducted a semi-natural experiment in a network of twelve wildflower strips and manipulated trophic structure (reduction of herbivorous molluscs and reduction of major predators) and plant diversity (2, 6, 12, 20 and 24 sown species; Figure 3).

Figure 2. The 24 plant species of the wildflower strip see mixture. From left to right: *Pastinaca sativa*, *Fagopyrum esculentum*, *Legusia speculum-veneris*, *Onobrychis viciifolia*, *Daucus carota*, *Dipsacus fullonum*, *Centaurea cyanus*, *Papaver rhoeas*, *Melilotus albus*, *Hypericum perforatum*, *Malva sylvestris*, *Tanacetum vulgare*, *Verbascum lychnitis*, *Agrostemma githago*, *Centaurea jacea*, *Echium vulgare*, *Origanum vulgare*, *Leucanthemum vulgare*, *Anthemis tinctoria*, *Silene latifolia*, *Cichorium intybus*, *Achillea millefolium*, *Verbascum thapsus*, *Malva moschata*. Plant species in grey were used only in the 24 species plots in the plant diversity experiment.

Figure 3. Experimental wildflower strips in an intensively-used agricultural landscape in a) the first year after sowing, with fence treatments and trap nests, and b) the second year after sowing. Photo by O.Bruggisser.

STUDY ORGANISMS

SLUGS

Severe damage of crops adjacent to wildflower strips has been recorded, especially by two slug species, *Arion lusitanicus* Mabille and *Deroceras reticulatum* Müller (Frank 1998a). *Arion lusitanicus* is native to Southern Europe but is now invasive across Europe (Schmid 1970). It prefers open areas and has become a severe pest in arable land in the last decade (Frank 1998b; Grimm 2001). Densities of more than 50 individuals per square metre have been observed in wildflower strips (Grimm 2001). Slugs of the genus *Deroceras* are pests in agricultural areas all over the world (Clemente *et al.* 2008), but are native to central Europe (Kerney *et al.* 1983). The slugs are known to feed on plants of the wildflower mixture (Frank 2003). However, slug numbers might be reduced by ground beetles and vertebrate predators, with effects on vegetation in turn (Buckland & Grime 2000). The mollusc community in wildflower strips and in particular its relationship to plant composition, diversity and structure is poorly understood. We monitored the mollusc community in wildflower strips using tile plates where molluscs could take shelter (Figure 4).

Figure 4. Tiles (size 30 x 30 cm) used as surface traps (at the left hand side) where molluscs could take shelter.
Photo Y.Fabian.

SOLITARY WILD BEES AND WASPS

Solitary aculeate bees and wasps (Hymenoptera: Aculeata) construct nests in a variety of locations, using a wide range of nesting materials. Some species build free-standing nests of mud attached to rocks, plants, or human structures. Others excavate tunnels in soil or plant materials, such as rotten wood or pith-filled plant stems. Finally, the so-called "cavity-nesters" seek out existing cavities, commonly either hollow plant stems or tunnels left by emerging wood-boring insects. Cavity-nesting females usually modify nest cavities by adding partitions and plugs consisting, in different species, of mud, plant resins, fresh or dried plant materials, or debris gathered from the environment. In this way they construct nests that consist of several brood cells each containing one larva and its food provision (Figure 5). Cavity-nesters have long been studied with the use of "trap nests", whose basic design consists of either natural tubes made from hollow, dried plant stems, such as reed internodes of *Phragmites australis*, or artificial tunnels such as paper straws or holes drilled in wood (Krombein 1967).

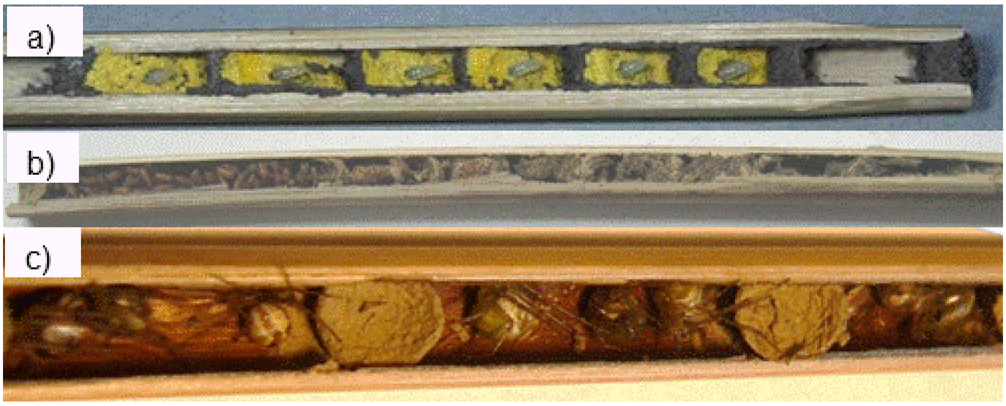

Figure 5. Brood cells in reed internodes containing a) bee eggs (*Osmia bicornis*), separated by mud partitions, with pollen provided as larval food; b) parasitized brood cells of the same bee species with pupal cocoons of the clepto-parasitic drosophilid fly *Cacoxenus indagator*, at the entrance of the straw (left hand side) and c) brood cells built by the spider-predating sphecid wasp *Trypoxylon figulus*, filled with spiders. Photos by P.Westrich, Y.Fabian, O.Bruggisser.

Wild cavity-nesting bees (Apidae) act as pollinators and collect pollen or nectar as food for their larvae (Westrich 1989; Gathmann & Tscharntke 1999a, Figure 5a). Cavity-nesting wasps belong to the families Eumenidae, Sphecidae and Pompilidae and can act as biological control agents by collecting herbivorous arthropods of lower trophic levels (Tscharntke *et al.* 1998), including phloem-sucking aphids (Aphididae), or larvae of smaller moths (microlepidoptera), leaf beetles (Chrysomelidae), weevils (Curculionidae) but other wasp species feed on spiders (Araneae; see Figure 5c and 8), which represent higher trophic level arthropods that can be beneficial as predators in agricultural ecosystems (Schmidt-Entling & Dobeli 2009). Thus, cavity-nesting wasps can be separated into three functional groups according to their trophic guilds, as predators of aphids, other herbivores, or spiders, to account for the ecological role of their prey.

In Switzerland, 616 bee species have been recorded, about half of which are ground-nesting, about 25% nest in above-ground cavities and 25% are brood parasites, all belonging to the Apidae (Amiet *et al.* 2007). More than 30 of the cavity-nesting bee species can be recorded in standardized trap nests (Figure 6), as well as more than 30 sphecid, 20 eumenid and five pompilid wasps (Gathmann & Tscharntke 1999b).

All these host species can be attacked by a diverse set of enemies, including Hymenoptera (clepto-parasites and parasitoids), Diptera (parasites, Figure 5b), Coleoptera (predators) and Acari (parasites). For example, *Osmia bicornis* (Figure 5a and 8), the most abundant bee species in trap nests in temperate agro-ecosystems, can be attacked by more than ten different species, spanning a range between specialists and generalists. Trap nests therefore offer insights into multi-trophic effects of experimental changes at local and regional scales with implications for ecosystem functioning in agricultural landscapes.

Figure 6. Standardized trap nest consisting of 150-180 *Phragmites vulgaris* internodes in a plastic pipe covered with a wooden roof for the colonization of cavity-nesting bees, wasps and their enemies. Photo by O.Bruggisser.

AIMS OF THE STUDY

Our study was conducted at two different spatial scales. The aim on a small scale was to compare the effect of plant diversity, structure and composition on the functional groups of herbivores and pollinators, biological control agents and their enemies in wildflower strips (**Chapters 2** and **3**). On a larger scale, the aim was to compare the importance of landscape composition, spatial arrangement, and vegetation on pollinators, biological control agents and their enemies and the complexity and structure of their food webs (**Chapter 4**).

In our study, we conducted a semi-natural experiment in a network of twelve wildflower strips in intensive agricultural landscape. We manipulated trophic structure (reduction of herbivorous molluscs and reduction of major predators) and plant diversity (2, 6, 12, 20 and 24 sown species) on a small scale, to assess the effect of plant diversity, biomass and composition on different functional groups of invertebrates that are of specific importance for agriculture. On a landscape scale our strips were placed along a gradient of landscape heterogeneity and isolation. This design allowed us to assess the effect of vegetation and landscape on a variety of communities relevant for agricultural ecosystems.

In the first part of this thesis, we investigated the effect of plant diversity, biomass and composition on herbivorous molluscs (Figure 7), and *vice versa*, the effect of mollusc abundance on vegetation.

Figure 7. The slug *Arion lusitanicus*, an abundant mollusc species in agricultural landscapes.
Photo by H. Fabian.

In the second part of this thesis, we aimed to identify the small-scale effect of plant species richness, structure and composition on different functional groups of cavity-nesting wild bees, wasps, their enemies, prey and the underlying food-web structure in trap nests (Figure 8).

Figure 8. The most common species in four functional groups of hosts in trap nests (from left to right): bees (*Osmia bicornis*), aphid-predating wasps (*Passaloecus borealis*), herbivore-predating wasps (*Ancistrocerus nigricornis*), and spider-predating wasps (*Trypoxylon figulus*).

In the third part, we constructed food webs with quantitative trophic links and compared food-web structure among wildflower strips (Figure 9) to identify the importance of vegetation characteristics, spatial arrangement, landscape composition, and landscape heterogeneity for trap-nesting bee and wasp communities.

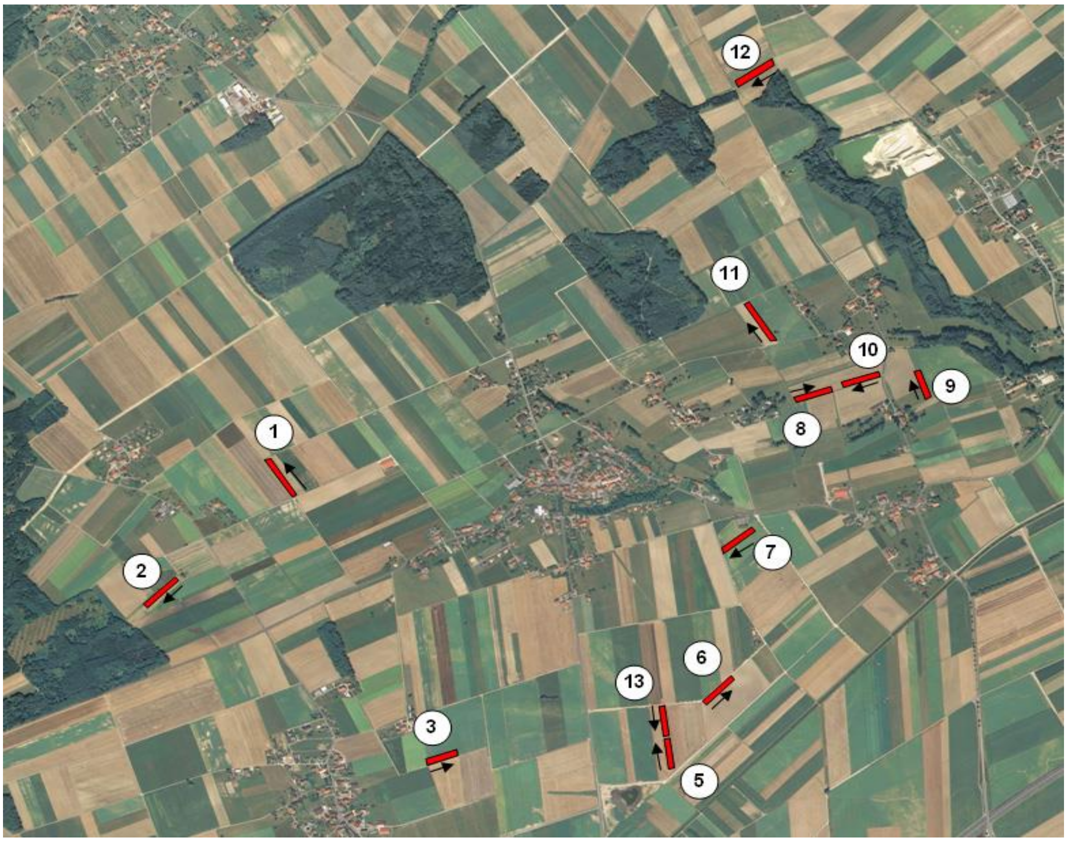

Figure 9. Aerial photo of the study area. The 12 sown experimental wildflower strips are marked in red, with arrows pointing towards the conventional wildflower mixture block at the end of each strip.

Chapter 2

Diversity protects plant communities against generalist molluscan herbivores

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published in Ecology and Evolution (2012)

ABSTRACT

Wildflower strips are used to increase natural enemies of crop pests and to conserve insect diversity on farmland. Molluscs, especially slugs, can affect the vegetation development in these strips considerably. While recent theoretical work suggests that more diverse plant communities will exhibit greater resistance against herbivore pressure, empirical studies are scarce. We conducted a semi-natural experiment in wildflower strips, manipulating trophic structure (reduction of herbivorous molluscs and reduction of major predators) and plant diversity (2, 6, 12, 20 and 24 sown species). This design allowed us to assess the effect of plant diversity, biomass and composition on molluscs, and *vice versa*, the effect of mollusc abundance on vegetation. Seven species of molluscs were found in the strips, with the slugs *Arion lusitanicus*, *Deroceras reticulatum* and *D. panormitanum* being most frequent. We found a negative relationship between plant diversity and mollusc abundance, which was due predominantly to a decrease of the agricultural pest species *A. lusitanicus*. These results are consistent with the hypothesis that plant diversity can reduce the impact of herbivores. However, plant identity also had an effect on molluscs, and accounted for a much larger fraction of the variation in mollusc communities than biodiversity effects. While overall plant diversity decreased during the three years of the study, in the final year the highest plant diversity was found in the plots where mollusc populations were experimentally reduced. We conclude that selective feeding by generalist herbivores leads to changes in plant community composition and hence reduced plant diversity. Our results highlight the importance of plant biodiversity as protection against generalist herbivores, which if abundant can in the long term negatively impact plant diversity, driving the system along a "low plant diversity – high mollusc abundance" trajectory.

Keywords: Agroecosystem, Biodiversity, Ecosystem functioning, Gastropoda, Herbivory, Plant composition, Resource concentration hypothesis

INTRODUCTION

Declining global biodiversity has inspired a large number of studies analysing the effects of plant diversity on the diversity and abundance of higher trophic levels and on ecosystem functioning (e.g.Tilman *et al.* 1997b; Cardinale *et al.* 2006; Haddad *et al.* 2009; Scherber *et al.* 2010a). Two contrasting hypotheses focusing on plant-herbivore interactions have been formulated. The *more individuals hypothesis* (Srivastava & Lawton 1998) suggests that diverse plant communities are often more productive than simple plant communities (Tilman *et al.* 2001) and provide a greater quantity of resources for consumers, thereby increasing their number. Further, herbivores may also increase their consumption and biomass when feeding on a more diverse plant community, as is the case in grasshoppers (Pfisterer *et al.* 2003; Unsicker *et al.* 2008). While the *more individuals hypothesis* assumes a similar effect on all herbivore species, the *resource concentration hypothesis* (Root 1973) makes a prediction only for specialist herbivores: specialist populations are expected to increase when their food plants are at high abundance. Therefore, species-poor plant communities should show higher specialist herbivore abundances than diverse plant communities where host plants are more dispersed. Hence there is a lower risk of specialist herbivory in species-rich plant communities. The situation is less clear for generalists, although they can also show feeding preferences (Scherber *et al.* 2010b) and thus should respond to changes in plant composition.

Vegetation characteristics other than plant diversity and composition are also important for the abundance and species richness of herbivores. For example, dense vegetation may serve as hiding-place from enemies (Jeffries & Lawton 1984), cover from the sun (Archard *et al.* 2004), or nesting place (Briner *et al.* 2005). High plant biomass may also ensure high food availability and cover over time. The *plant architecture hypothesis* (Lawton 1983) states that the physical structure of the aerial parts of the host plant influences the community structure of herbivorous insects, resulting in greater herbivore abundances in stands with more complex structure and greater biomass (Riihimaki *et al.* 2006; Randlkofer *et al.* 2009). However the relative importance of plant diversity, composition and structure for the herbivore community in natural ecosystems has not been quantified in earlier studies.

The herbivore community can, in turn, affect plant diversity and community composition by selectively feeding upon particular species and altering competitive interactions (Buckland & Grime 2000; Buschmann *et al.* 2005; Howe *et al.* 2006; Scherber *et al.* 2010b; Allan & Crawley 2011). Herbivory can affect plant diversity positively, negatively, or neutrally, depending on the herbivore species and habitat type. Herbivorous molluscs like slugs are known to alter plant species richness and composition, by selectively feeding on plant seedlings. They also have the potential to alter plant biomass, as has been shown in microcosm experiments (Buckland & Grime 2000; Buschmann *et al.* 2005; Lanta 2007). However, the effect of molluscs on the vegetation of species-rich natural ecosystems is less well understood (but see Hanley *et al.* 1995; Allan & Crawley 2011).

Due to intensification of agriculture, a drastic loss of biodiversity has occurred in agro-ecosystems in the second half of the 20th century (Kruess & Tscharntke 1994; Tscharntke *et al.* 2005). To counter species decline, agro-environmental schemes were introduced across Europe, with payments to farmers and other landholders to address environmental problems or to promote environmental amenities (OECD 2003). More than a decade has passed since their introduction, and studies of the ecological effectiveness of such schemes have shown both positive and negative impacts (Kleijn & Sutherland 2003; Knop *et al.* 2006; Haaland *et al.* 2011). For farmers, benefits include the establishment of pollinators and biological control agents (Haaland *et al.* 2011; Pywell *et al.* 2011), but there is also the risk that they will foster herbivorous pests such as molluscs (Frank 1998a) or voles (Briner *et al.* 2005).

Wildflower strips are one form of agro-environmental scheme. In the Swiss lowlands they are made up of a recommended wildflower mixture containing 24 herbaceous species (Schaffner *et al.* 1998) sown inside agricultural fields or along their edges, and maintained for six years (Nentwig 1992). The wildflower species were chosen to benefit a maximal number of taxa, including arthropods that play an important role in pollination (Carvell *et al.* 2007) and biological control (Nentwig 1992). However, the strips are also favourable habitats for molluscs (Briner & Frank 1998; Keller *et al.* 1999; Günter 2000; Frank 2003) and micromammals (Aschwanden *et al.* 2007), because several of the plant species included are eaten by these groups and also provide dense cover, which offers reproduction sites and protection (Briner & Frank 1998). Severe slug damage of crops adjacent to wildflower strips has been recorded, especially by *Arion lusitanicus* Mabille and *Deroceras reticulatum* Müller (Frank 1998a). *Arion lusitanicus* (Figure 1b) is native to Southern Europe but is now invasive across Europe (Schmid 1970). It prefers open areas and has become a severe pest in arable land in the last decade (Frank 1998b; Grimm 2001). In some habitats (wildflower strips and meadows) densities of more than 50 individuals per square metre have been observed (Grimm 2001). Slugs of the genus *Deroceras* are pests in agricultural areas all over the world (Clemente *et al.* 2008), but are native to central Europe (Kerney *et al.* 1983).

The mollusc community in wildflower strips and in particular its relationship to plant composition, diversity and structure is, to our knowledge, poorly understood. In a 3-year experiment where sown plant number and mollusc abundance were manipulated, we first studied the importance of plant diversity, structure, and composition on the abundance of molluscs and especially slugs; secondly, we estimated the effect of molluscs on the plant community. We addressed the following specific questions: (1) Are species-rich plant communities more resistant to mollusc invasion than species-poor communities? (2) Is vegetation structure, plant diversity or plant composition more important to understand the structure of mollusc communities? (3) Do herbivorous molluscs have the potential to alter plant diversity, structure and composition in wildflower strips and, if so, what functional groups and species of plants are most affected?

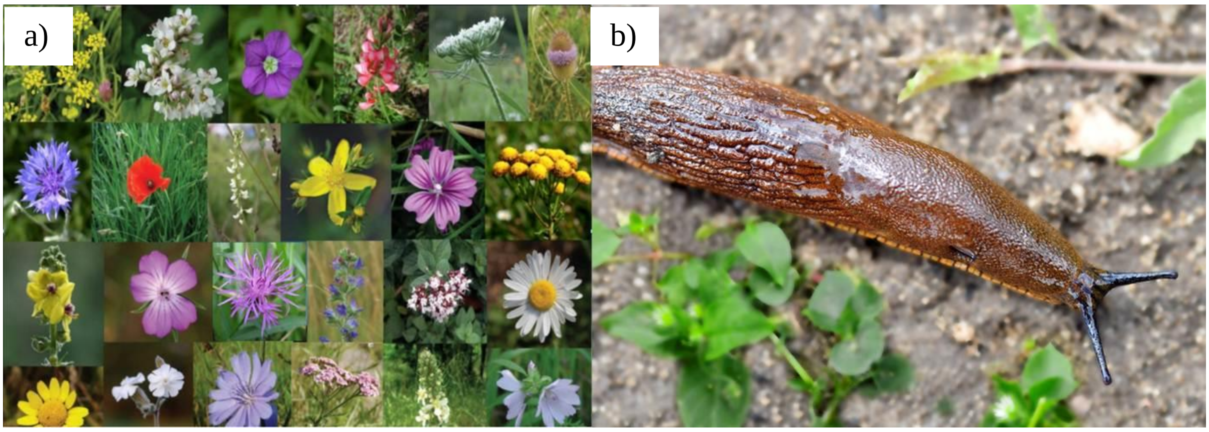

Figure 1. Photographs of the 24 plant species used in wildflower strips and of *Arion lusitanicus*, the most abundant mollusc species. Photo by H. Fabian.

METHODS

FIELD MANIPULATIONS

In spring (April-June) 2007 twelve wildflower strips were sown in field margins around the village of Grandcour, 10 km south of Lake Neuchatel in northwest Switzerland (479 m above sea level; coordinates: 46° 52' N 06° 56' E). Annual average temperature is 10.1 °C, average annual precipitation amounts to approximately 941 mm (Confederation 2011). The region is characterized by a mosaic of arable fields (intensive agriculture), grasslands and forests.

Each wildflower strip was divided into four plots of 216 m^2; one plot was sown with the full conventional wildflower mixture of 24 plants that farmers use in Central Switzerland (Günter 2000, see Figure 1a); the remaining three plots were randomly assigned to one of three treatments: (1) fence with 25 mm mesh size, (2) fence with 8 mm mesh size and molluscicide application, (3) no fence. Within each of these three plots, we established four

6 x 9 m subplots differing in sown plant number (2, 6, 12, 20 sown species randomly assigned to the subplots, Figure 2).

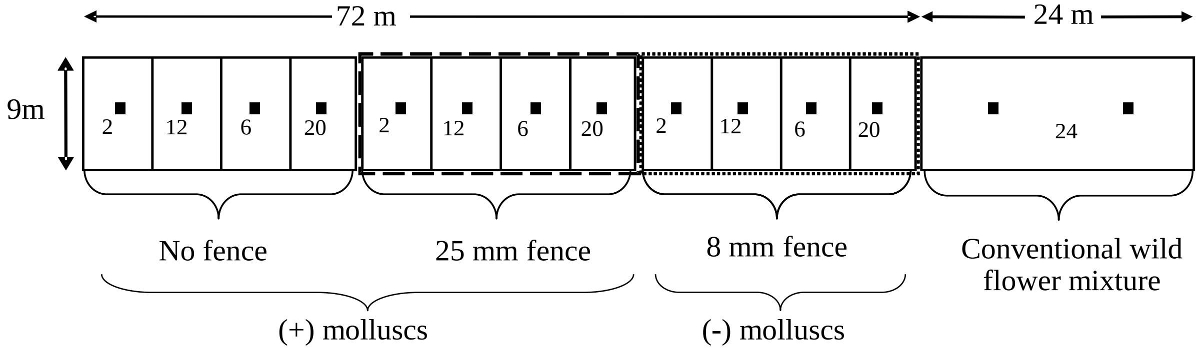

Figure 2. Layout of experimental wildflower strips with mollusc tile traps along the centre (black circles). Numbers in the subplots indicate sown plant species number; dashed line represents a fence with 25 mm mesh size, dotted line with 8 mm mesh size.

The plant species composition of each subplot was chosen by constrained random draw from a pool of 20 plant species with regard to equal frequency of occurrence in the 12 wildflower strips. We selected only species that belonged to the same functional group, tall herbs, to manipulate plant diversity only and not functional group diversity. We excluded two small herbs, *Legusia speculum-veneris* and *Fagopyrum esculentum,* the latter not native to central Europe and two legumes, *Melilotus albus* and *Onobrychis viciifolia,* to prevent any possible bias through soil differences between subplots (Appendix Table S1; www.ufasamen.ch). Density of seeds corresponded to the official Swiss recommendations for sowing wildflower strips (Günter 2000). In contrast to other biodiversity experiments like Cedar Creek (Tilman *et al.* 1997b), BIODEPTH (Otway *et al.* 2005) or The JENA Experiment (Roscher *et al.* 2004), our experimental plots were not weeded to avoid disturbance, with the exception of the problematic weeds *Cirsium arvense* and *Rumex obtusifolius*, and,additionally in the first year (2007) *Chenopodium album* and *Amaranthus retroflexus* to prevent light competition during germination. Otherwise, plant communities were the result of self-assemblage following initial sowing.

The fencing treatment was intended to manipulate the densities of large vertebrate predators (reduced numbers in 25 mm and 8 mm fenced plots), and of micromammals and molluscs (reduced numbers in 8 mm fenced plots). However, only molluscs were successfully controlled in the 8 mm fenced plots (hereafter called "(-) mollusc"). Populations were reduced by application of 0.02 kg/m^2 METAREX® (DE SANGOSSE, 47480 Pont du Casse, SA France), a 5% metaldehyde slug bait (Frank 1998b) every two weeks along the inside of the 8 mm fence, between mid-March and late October during the three years of the study. To avoid any confounding effect of metaldehyde pellets on seedling community composition and hence diversity, we applied molluscicides only along the inside of the 8 mm fence, and on the 30 cm wide central path (used to walk in the subplots), hence about 90% of the plot was unaffected. Furthermore, studies of the effect of metaldehyde on vegetation did not reveal any impact (Hector *et al.* 2004). Despite fencing and continuous live trapping of micromammals in 2007 and 2008, their density was not reduced. In 2009, a study of common voles (*Microtus arvalis*) and wood mice (*Apodemus sylvaticus*) revealed marginally greater abundances in 8 mm plots compared to 25 mm and control plots (replicated G-test, P = 0.108 and P = 0.098, respectively, Meyer 2011). Extensive observations during night and day revealed that vertebrate predators (foxes, hedgehogs and birds of prey) very rarely entered wildflower strips, even when unfenced (Gregoire Schaub, pers. comm.). For this reason, we merged in the present study the treatments "25 mm fence" and "no fence", hereafter called "(+) mollusc". We found no effect of the fencing treatment on other animal species, notably on slug predators like carabid beetles (Y. Fabian unpubl. data).

PLANT DATA

In each subplot (Table S1), all plant species were identified and their individual percentage cover visually estimated using the standard method of Braun-Blanquet (Perner *et al.* 2005) in autumn 2007, 2008 and 2009. *Plant diversity* was characterized by species richness and the effective number of species. Species richness corresponds to the total number of plant species. The effective number of species (Jost 2006) is based on Shannon diversity and expresses species richness corrected for relative abundance – in our case, relative cover of plants.

Vegetation structure was characterized by the average vegetation height and plant biomass. Vegetation height was estimated as the average height of all plants of a subplot. Plant biomass was assessed with two different methods: in spring 15.4. - 28.5.2008 we cut to ground level all plants in five squares of 30 cm per subplot. Samples were bagged and oven dried at 60 °C to constant weight. We took the average weight of the five samples per subplot. In later periods this method became too work intensive because of the height of the vegetation (often > 2 m). In early autumn 2008 and 2009, we measured the leaf area index (LAI) with a LAI-2000 (LI-COR Biosciences) at 24 random points in each subplot, and calibrated the method with 5 biomass samples from 8 and 16 subplots in 2008 and 2009, respectively. The resulting linear relationship (*2008*: Pearson product-moment correlation $r = 0.89$ and *2009*: $r = 0.87$) was used to transform the average LAI values to plant biomass per subplot in g/m^2.

The plant species were split into five functional groups: small herbs (< 60 cm), tall herbs (> 60 cm), legumes, grasses and small trees (Roscher *et al.* 2004). We used the number of species of the different plant functional groups and the cover of the plant functional groups in our analysis.

MOLLUSC DATA

The abundance of molluscs was estimated using tiles (size 30 x 30 cm) as surface traps where molluscs could take shelter (Archard *et al.* 2004). We used 14 tiles per wildflower strip (Figure 2), one in each subplot and two in the 24-species plot, laid on bare ground in August 2007. In the (-) mollusc plots, any molluscs and eggs found under the tiles were removed once in spring, summer and autumn to maintain their exclusion. We sampled molluscs in September 2007, and in June and September 2008 and 2009. Species were determined following Kerney *et al.* (1983). Molluscs were counted and the length (b in cm) and width (a in cm) of each individual measured. Body volume (V in cm^3) was calculated using the equation for a prolate spheroid:

$$V = \frac{4}{3}\pi a^2 b,$$

to analyse the average body volume per species, per plot and subplot over the five different sessions. Additionally, we estimated the number of mollusc eggs under the tiles.

During the three years of the experiment, ants (Formicinae) increasingly established colonies underneath the tiles. The percentage cover of ant brood was estimated from digital photos as a measure of ant abundance.

CLIMATE DATA

To account for short-term effects of climate on mollusc abundance, the sampling was carried out on sunny days with air temperatures exceeding 12 °C. We controlled for climate variability by using climate measurements taken hourly from the Agrometeo website (Confederation 2011) for the meteorological station Delley, which lies 2-5 km from the experimental sites. For each sampling session, mean air temperature (T in °C), mean air humidity (H in %), and a quadratic term to model their optimum (T^2, H^2) were included in all statistical models.

STATISTICAL ANALYSES

All analyses were carried out using R version 2.12.0 (R Development Core Team 2012). Plant species richness was log transformed, percentage cover of plant species was square root transformed, and proportion of ant nest cover was arcsine square root transformed to correct for non-normality and heterogeneity of variance. Continuous explanatory variables were standardized to zero mean and unit variance using the function *scale* in vegan (Oksanen *et al.* 2011).

Effects of the vegetation on mollusc abundance

To test the effect of plant diversity and vegetation structure on mollusc abundance, we used the data from (+) mollusc plots only. The initial models included plant species richness, effective number of plant species, biomass, vegetation height, ant abundance, fence treatments, season and year as fixed effects and the twelve wildflower strips as random effects allowing for a random intercept. Weather conditions on the sampling day (T, T^2, H and H^2) were always included in the models to control for short-term effects of the climate (for the weather effect on slugs, see Table S4). The total abundances of molluscs, mollusc eggs and the individual slug species were modelled with the function *glmmadmb* in the package glmmADMB, fitting a zero-inflated negative binomial distribution (Zuur *et al.* 2009). We excluded the weather variables in the models for the slug eggs. All variables were included in the full model and the non-significant terms ($P < 0.05$) excluded in a backward stepwise procedure to select the simplest model. The function *glht* of the package multcomp (Hothorn *et al.* 2008) was used to compute the difference between years and thus allow multiple comparisons for parametric models. The analyses were performed firstly with plant species richness, secondly with species richness of the four plant functional groups (tall herbs, small herbs, grasses and legumes), and thirdly with the cover of the functional groups. Note that we excluded the "tree" functional group in this analysis because there were only 5 species with very low cover (0.09%) in 2009 only. The body masses of the three most abundant mollusc species were analysed with linear mixed effect models using *lme* (Pinheiro *et al.* 2011). Here we simplified full models by removing non-significant terms using the function *stepAIC* with forward and backward elimination (Venables & Ripley 2002).

Mollusc community structure

Canonical correspondence analysis (CCA) was performed in vegan (Oksanen *et al.* 2011) to analyse the response of the mollusc community to plant diversity (species richness and effective number of species), vegetation structure (vegetation height and plant biomass) and plant composition (log transformed and scaled cover of the 30 most abundant plant species). Mollusc species that occurred in only one subplot (i.e., singletons) were excluded. Furthermore, we excluded all data from the (-) mollusc plots and included the 24-species plots. In all permutation tests between the environmental variables and mollusc community structure, 9999 constrained permutations were performed using the wildflower strips and sessions as block variables.

We compared the explanatory power of the three sets of vegetation descriptors (diversity, structure and composition) by partitioning the variation of the mollusc data (Hofer *et al.* 2000), using the function *varpart* in vegan (Oksanen *et al.* 2011). This application uses partial redundancy analysis (RDA) for community matrixes as independent variables and partial multiple regression analysis for vector-independent variables. Adjusted *R* square values were calculated since it is the only unbiased method (Peres-Neto *et al.* 2006). We used the first two correspondence analysis axes of the plant composition as variables, resulting in equal numbers of explanatory variables for each environmental set (sets of variables with more descriptors would otherwise be comparatively overvalued in partial analyses). This allowed us to calculate the percentage of variance due exclusively and in common to the three groups of descriptors. To test significance of the exclusive fractions, we applied a test with 9999 permutations using the function *anova* in *varpart*.

Effects of molluscs on the vegetation

The effectiveness of the (-) mollusc treatment was tested by analysing the total mollusc abundance, abundance of the three most common species and the mollusc eggs, using linear mixed effect models (*lme*) in the package nlme (Pinheiro *et al.* 2011), with the three fence treatments and the sown plant number as fixed effects and the twelve wildflower strips as random effect. Again, the function *glht* (Hothorn *et al.* 2008) was used to compute the difference between treatments and years.

We then analysed the effects of molluscs on the vegetation. First, the effect of the mollusc treatment and of sown plant number on the plant species richness, effective number of species, vegetation height, plant biomass, and number of invading plant species (species other than those from the sown seed mixture) were analysed for the three years separately, with the twelve wildflower strips as random variables. The species richness and cover of the plant functional groups and the individual cover of plant species were then analysed for 2009, the year in which plant diversity differences between the mollusc treatments were significant. We analysed only the 39 plant species that occurred in more than 20 out of the 144 subplots and that had a mean cover > 1% over all subplots in this year. We also analysed the presence ⁄ absence data for these plant species using linear mixed effect models with a binomial function and logit link (*lmer* in the package lme4), again using the mollusc treatments and sown plant number as explanatory variables and the twelve wildflower strips as random variables. To correct for multiple testing, we computed Q-values on the basis of the 39 P-values correcting for the false discovery rate (FDR = # of false positives / # of significant tests) using the library qvalue (Storey 2002). We fixed the tuning parameter λ to 0.0 (the most conservative value) for the presence / absence data and to a range between 0 and 0.9 for the cover data.

RESULTS

EFFECTS OF THE VEGETATION ON MOLLUSC ABUNDANCE

A total of 2772 molluscs of seven different species were found under the 144 tiles in the 12 wildflower strips over the five sampling periods, with slugs of the species *Arion lusitanicus* (Mabille), *Deroceras reticulatum* (Müller) and *D. panormitanum* (Lessona & Pollonera) accounting for 99% of all individuals (Table 1). The abundance of molluscs was significantly correlated with the number of mollusc species ($r = 0.63$, P-value < 0.001). There was large seasonal variation in slug abundance, with *A. lusitanicus* more common in spring and the two *Deroceras* species in autumn (Table 1 and Table 2). Superimposed on this seasonal variation was a steady increase in the abundance of *A. lusitanicus*, while the abundances of the *Deroceras* species were highest in 2008 (Table 1).

Table 1. Absolute abundance and mean volume ± s.d. (cm^3) of molluscs and their eggs. Data come from 168 tiles for 5 trapping sessions.

Species	2007	2008		2009		Sum abund-ance	Mean Volume ± s.d. (cm^3)
	Autumn	Spring	Autumn	Spring	Autumn		
Arion lusitanicus	10	164	100	457	337	1068	3.61 ± 2,80
A. rufus	0	0	3	0	0	3	32.72 ± 0.00
Deroceras reticulatum	364	57	473	9	241	1144	0.36 ± 0.27
D. panormitanum	110	4	292	5	115	526	0.21 ± 0.20
Cepaea hortensis	0	0	0	2	1	3	0.35 ± 0.15
C. nemoralis	0	0	0	0	1	1	4.19 ± 0.00
Trichia hispida	0	0	20	2	5	27	0.13 ± 0.06
Mollusc eggs	100	0	6222	0	5493	11815	-

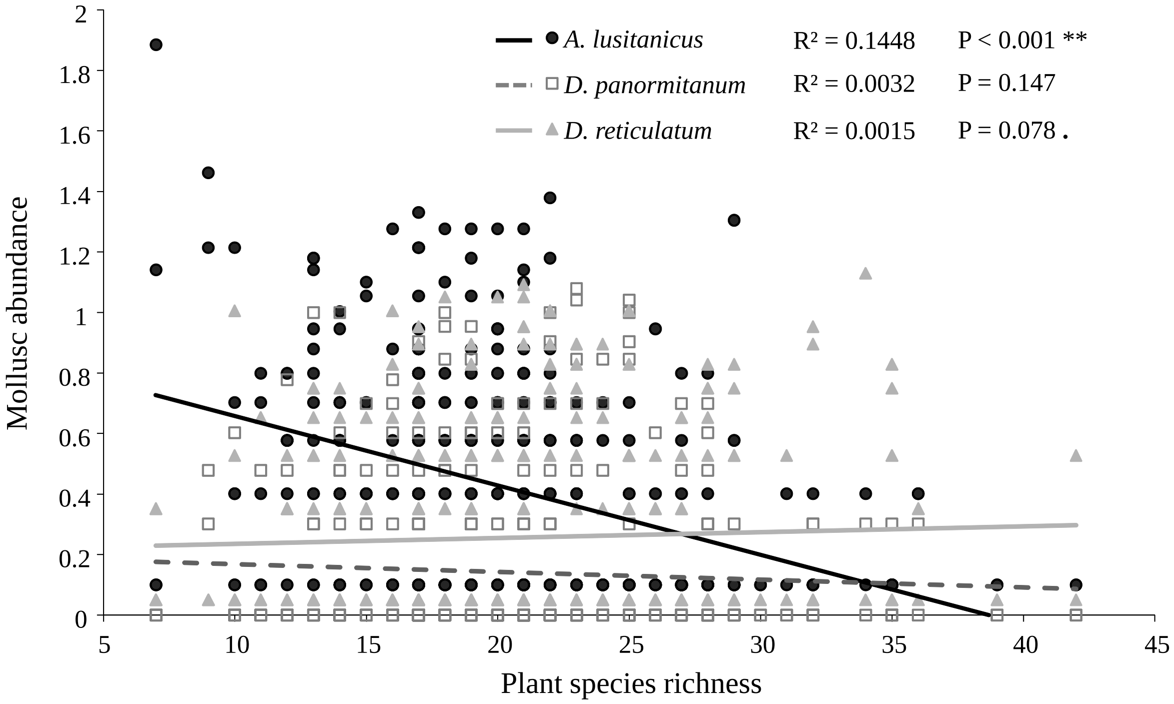

Figure 3. The relationship between plant species richness and mollusc abundance (log transformed) for *Arion lusitanicus* (black circles and line, to avoid over-plotting, a value of 0.1 was added), *Deroceras reticulatum* (light grey triangles and light grey line, a value of 0.05 was added) and *Deroceras panormitanum* (white squares and striped line), over the two seasons of the years 2008 and 2009, within the (+) mollusc plots. Regression lines give the fitted linear model for each species. Significances calculated using linear mixed effect models.

Total mollusc abundance was negatively correlated with plant species richness and ant abundance and positively correlated with vegetation height (Table 2; Figure 3). Mollusc abundance was also negatively correlated with the number of small herb species and their cover (Table 2). The three mollusc species showed different responses to the vegetation characteristics. The abundance of *A. lusitanicus* was negatively correlated with plant species richness in general and specifically with the number of legume and tall herb species (Table 2). The abundance of *D. panormitanum* was positively correlated with plant biomass, and negatively correlated with the small herb cover, whereas *D. reticulatum* was positively correlated with vegetation height and the number of tall herb species, and negatively correlated with grass cover. The effective number of plant species was not correlated with the abundance of any mollusc species. The abundance of mollusc eggs was positively correlated with plant biomass only.

The body mass of the three slug species was not influenced by plant species richness, effective number of species, vegetation height, or the treatments (Table S2). Only the body mass of *A. lusitanicus* was positively correlated with plant biomass.

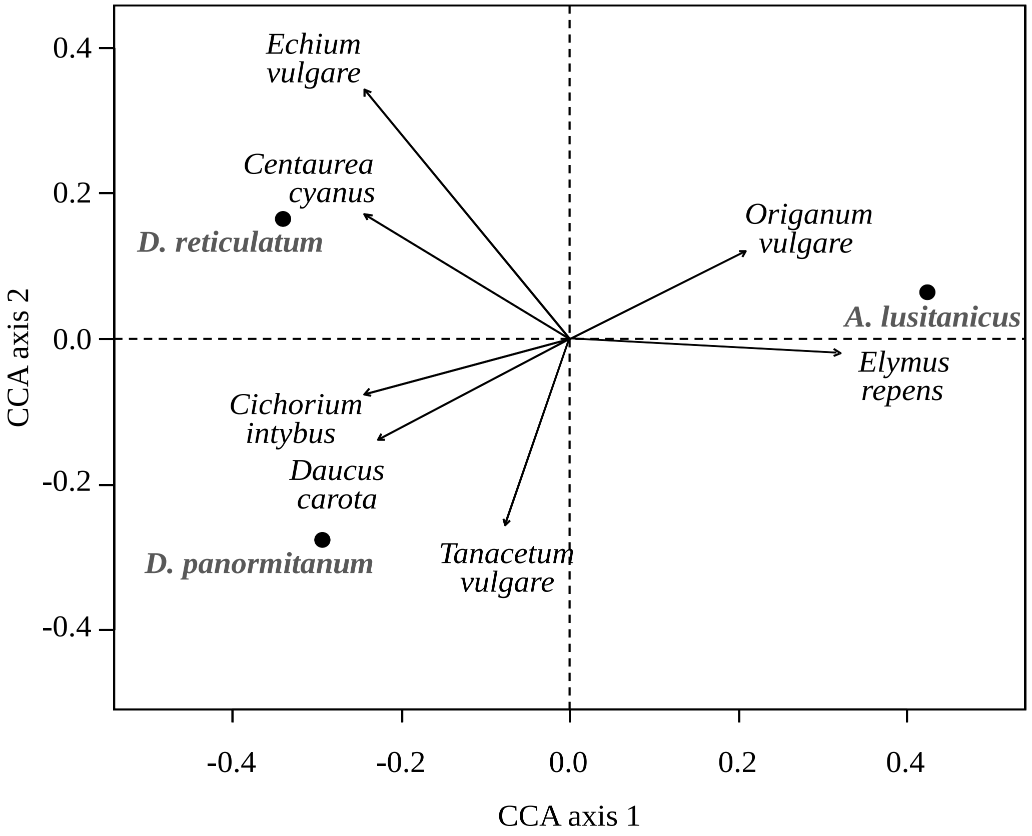

Figure 4. Canonical correspondence analysis biplot of mollusc community variation (large font italics in grey) dependent on plant species composition (small font in black). Among the 30 most abundant plant species, only those significantly related to mollusc community composition are shown. CCA axis 1 Eigenvalue = 0.195 and CCA axis 2 Eigenvalue = 0.049.

MOLLUSC COMMUNITY

Constrained ordinations revealed that the mollusc community was significantly influenced by *Centaurea cyanus*, *Cichorium intybus*, *Daucus carota*, *Echium vulgare*, *Tanacetum vulgare*, *Elymus repens* (all $P < 0.005$) and *Origanum vulgare* ($P = 0.015$; Figure 4). The first five tall herb species were strongly positively associated with the two *Deroceras* species, while the last two species (a grass and a tall herb) were associated with the *Arion* species. The two slug genera separate along the first CCA axis, which explains the greatest part of the data (19.5%). The partial correspondence analysis of the determinants of the mollusc community showed that plant composition explained a total of 23.2% of the variation, and 8.7% exclusively (Figure 5). It thus had much greater importance than plant diversity and plant structure, which explained a total of 16.9% and 1.1%, and exclusively 1.7% and 0.5%, respectively. The three sets of descriptors explained 26.2% of the total variation.

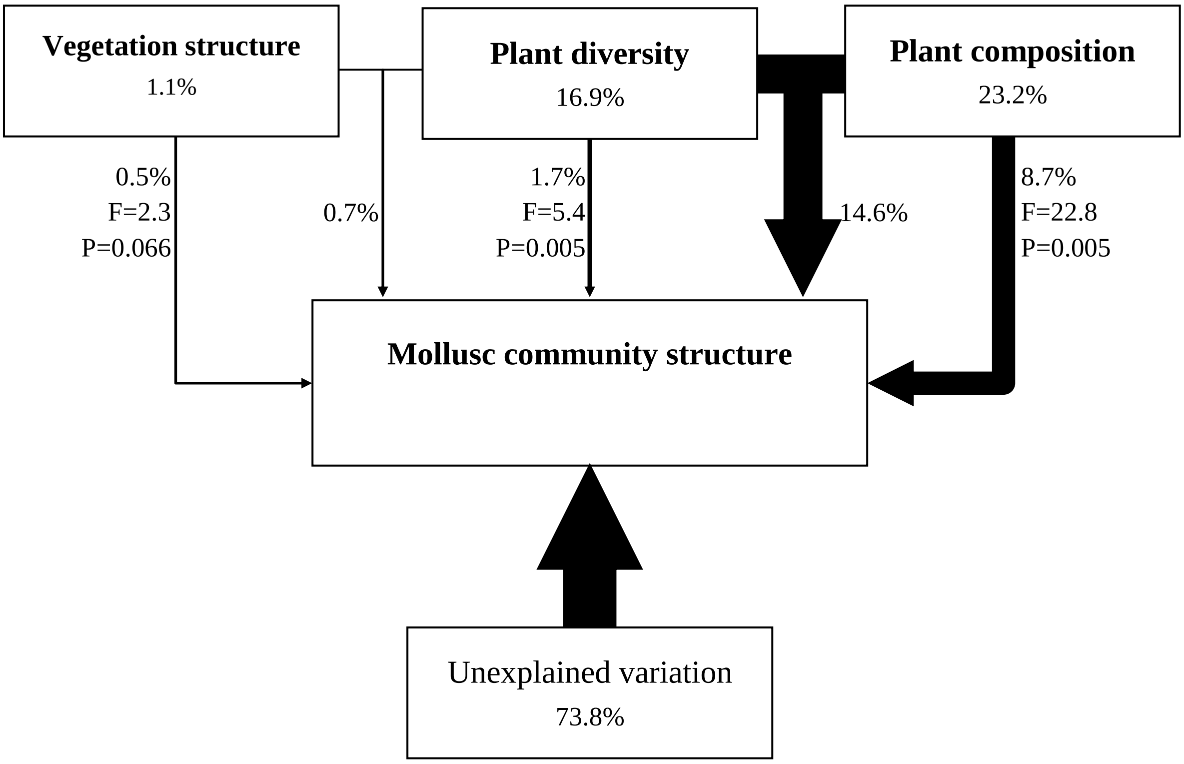

Figure 5. Variation partitioning of plant measures to explain mollusc community structure; numbers in percent represent the explained variation. Two variables describe each vegetation characteristic: average vegetation height and plant biomass for vegetation structure, number of plant species and effective number of plant species for plant diversity, the two first ordination axes of the 30 most abundant plant species for plant composition. Note that vegetation structure and plant composition share no common variation, and that only the three independent fractions can be statistically tested.

Table 2. Results from the mixed effect models for the total mollusc abundance, abundance of the three most common slug species and mollusc eggs.

	Season	Year	Ant abundance	Veg. height	Plant biomass	Plant species richness	Tall herb species	Small herb species	Legume species	Grass species	Tall herb cover	Small herb cover	Legume cover	Grass cover
All molluscs	A > S	**09>**07>08	-0.75 ***	0.1 *	-	-0.13 †	-	-0.17 *	-	-	-	-0.21 **	-	-
Arion lusitanicus	S > A †	09>08>**07**	-1.00 ***	-	-	-0.47 ***	-0.30 **	-	-0.36 **	-	-	-	-2.30 *****	-
Deroceras reticulatum	A > S ***	07>08>09	-0.30 *	0.2 *	-	0.19 †	0.23 **	-	-	-	-	-	-	-0.28 **
Deroceras panormitanum	A > S ***	**09>**07>08	-0.52 *	-	0.48 **	-	-	-0.23 †	-	-	-0.22 †	-0.49 ***	-	-
Mollusc eggs	A > S ***	09>08>**07**	-	-	0.24 **	-	-	-	-	-	-	-	-	-

Results from mixed models, as explained in the methods, with the slopes and significance for each response variable. Results for the variables that were excluded in a stepwise procedure from the full model are not shown (-).Plant diversity was log- and ant biomass arcsin / sqrt transformed. Multiple comparisons for parametric models were performed - levels of factors shown in bold are significantly different from other levels (P < 0.05); Seasons: A= autumn, S= spring, Years: 2007, 2008 and 2009; † P < 0.1, * P < 0.05, ** P < 0.01 and *** P < 0.001

EFFECTS OF MOLLUSCS ON THE VEGETATION

The reduction of molluscs by the fencing and molluscicide treatment was effective, with significantly lower abundances of molluscs and mollusc eggs in the (-) mollusc plots in 2008 and 2009 (Figure S1).

Across treatments, the mean number of plant species per subplot decreased from 32.7 (± 6.1; 19 - 45) in 2007, to 22.2 (± 6.5; 6-42) in 2008 and 19.3 (± 5.4, 7-35) in 2009 (standard deviation and range in brackets for the 12 strips, Figure 6). The sown plant species number was positively correlated with the total plant species richness ($r = 0.13$, $df = 280$, $P = 0.014$), and with the effective number of species ($r = 0.36$, $df = 280$, $P < 0.001$). Plant species richness was significantly greater in the (-) mollusc compared to (+) mollusc plots in the year 2009 (*lme* value = 0.17; df = 130; $P < 0.001$). In 2007 and 2008, the treatments did not differ (Figure 6). The relationship between plant species richness and biomass was not affected by mollusc herbivory in 2008 or 2009 (Figure 7). The number of invading plant species (the subplots were not weeded) was negatively affected by the sown species number in 2008 and 2009 (*lme* value = -0.14 and -0.12, df = 128 and 129, respectively; $P < 0.001$ in both years) and was higher in the (-) mollusc treatment only in 2009 (*lme* value = 0.16, df = 129, $P = 0.009$), with no significant interaction between sown species number and treatment in both years (Figure 8). There was no treatment effect on the effective number of species or vegetation height in any of the three years.

In 2009, the year in which effects on plant species richness were seen, there were significantly more tall herb and tree species in the (-) mollusc than in the (+) mollusc plots, and the cover of grasses and legumes was lower in (-) mollusc plots (Figure 9). When considering individual plant species, the presence and / or cover of eight tall herb species was significantly lower in (+) mollusc plots *(Achillea millefolium, Anthemis tinctoria, Cirsium arvense, Conyza canadensis, Echium vulgare, Daucus carota, Leucanthemum vulgare and*

Tanacetum vulgare), while the cover of *Dipsacus fullonum, Equisetum arvense, Dactylus glomerata, Lolium perenne* and *Trifolium repens* was significantly higher (Table 3).

Table 3. The effect of molluscs on the abundance of individual plant species.

Plant species	(+) mollusc	(-) mollusc	Mollusc effect	Q-Value
Tall herbs				
Achillea millefolium	0.64 ± 0.49	0.88 ± 0.33	-	0.014 *
Anthemis tinctoria	0.55 ± 0.50	0.77 ± 0.42	-	0.033 *
Cirsium arvense (cover)	0.67 ± 3.01	2.81 ± 8.21	-	0.043 *
Conyza canadensis	0.28 ± 0.45	0.48 ± 0.50	-	0.014 *
Echium vulgare	0.23 ± 0.42	0.52 ± 0.50	-	0.014 *
Daucus carota	0.43 ± 0.50	0.65 ± 0.48	-	0.014 *
Dipsacus fullonum (cover)	22.83 ± 24.14	15.96 ± 20.45	+	0.087 †
Leucanthemum vulgare	0.51 ± 0.50	0.73 ± 0.45	-	0.014 *
Leucanthemum vulgare (cover)	4.30 ± 9.21	12.23 ± 21.12	-	0.003 **
Tanacetum vulgare (cover)	4.89 ± 10.63	9.75 ± 15.23	-	0.043 *
Tanacetum vulgare	0.61 ± 0.48	0.83 ± 0.38	-	0.037 *
Grasses				
*Dactylus glomerata (*cover*)*	1.66 ± 5.89	0.83 ± 2.23	+	0.043 *
Equisetum arvense (cover)	0.71 ± 2.73	0.03 ± 0.10	+	0.077 †
Lolium perenne (cover)	3.30 ± 9.72	0.90 ± 2.80	+	0.046 *
Legumes				
Trifolium repens (cover)	0.48 ± 1.61	0.08 ± 0.52	+	0.098 †

Arithmetic means ± s.d. based on untransformed data of the cover (indicated with a "cover" after the name) and the presence / absence of plant species that were significantly affected by the mollusc treatment in 2009. Mollusc effect: + = cover/abundance of the specific plant species increases with the presence of molluscs, - = cover/abundance of the specific plant species decreases with the presence of molluscs. Q-values are P-values from mixed effects models corrected for multiple tests (see methods section). We tested the 39 most abundant plant species; non-significant results were obtained for: *Centaurea jacea, Origanum vulgare, Elymus repens, Malva moschata, Epilobium sp., Hypericum perforatum, Arrhenaterum elatius, Apera spica-venti, Verbascum lychnitis, Silene latifolia, Holcus lanatus, Pastinaca sativa, Rumex obtusifolius, Taraxacum officinale, Rubus sp., Cichorium intybus, Malva sylvestris, Melilotus albus, Linaria vulgaris, Verbascum thapsus, Lactuca serriola, Setaria pumila, Phleum pratense, Plantago major, Plantago lanceolata* and *Sonchus asper;* Significance of Q values*:* † Q < 0.10*,* * Q < 0.05*,* ** Q < 0.01 and *** Q < 0.001

DISCUSSION

In this semi-natural diversity experiment in wildflower strips over three years, we found evidence for a negative relationship between plant diversity and mollusc abundance, which leads to the conclusion that plant diversity can reduce the impact of herbivores (Root 1973). Moreover, plant identity had much greater importance than plant diversity as determinant of mollusc community composition. After three years, the highest plant diversity was found in the plots where molluscs were reduced, which is likely to result from selective feeding by molluscs leading to changes in plant composition and hence reduced plant diversity. Here we explore possible mechanisms behind our findings, outline their implications for biodiversity research in agro-ecosystems, and discuss experimental caveats of our study.

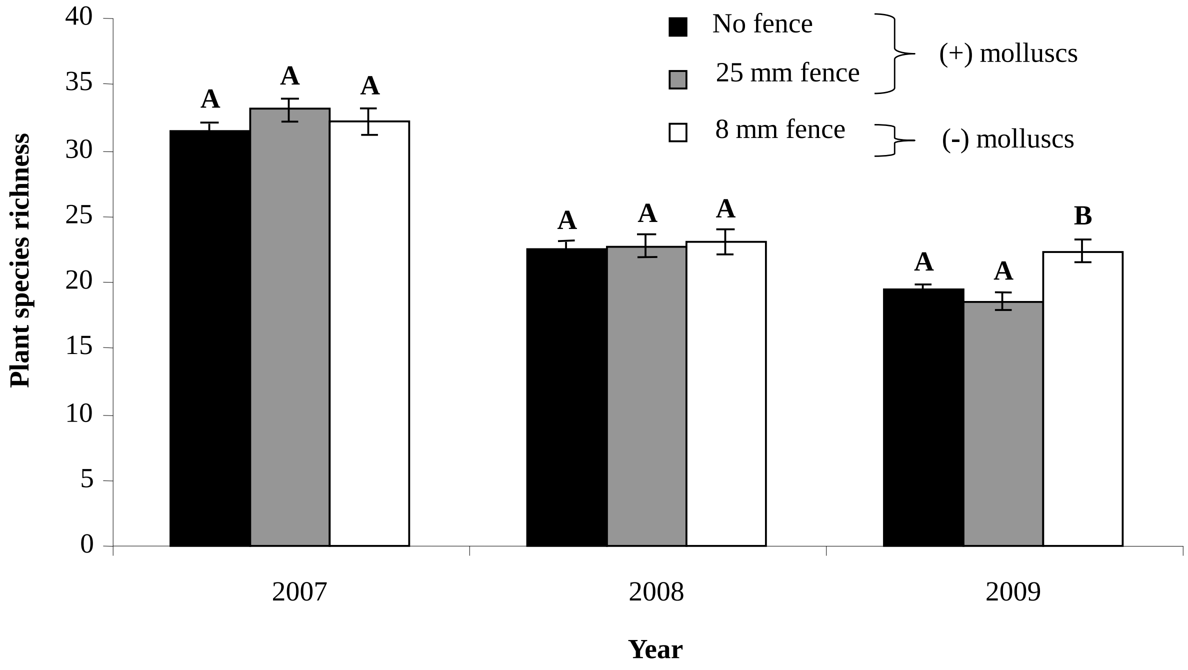

Figure 6. Average number of plant species for the three fence treatments for each year. Significant differences ($P < 0.05$) between fence treatments within a year are represented by different letters (A-B) calculated by multiple comparisons for parametric linear mixed effect models. Error bars represent the standard error of the mean from a total of 48 plots in the 12 wild flower strips.

Effects of the vegetation on mollusc abundance

We found a negative effect of plant species richness on slug abundance, which was mostly due to the lower abundance of *A. lusitanicus*. Hence we found evidence for the resource concentration hypothesis (Root 1973) for generalist herbivores. Our result is in contrast to Scherber *et al.* (2010a), who found that a higher plant species richness hosted more herbivores, in line with the *more individuals hypothesis*. Their finding, however, concerned total herbivore species richness and abundance, and it would be interesting to analyse the relationships at a species or group level, because some taxa may behave differently. Indeed, we found that the abundance of *D. reticulatum* slightly increased with increasing plant – and especially tall herb – diversity (Dedov *et al.* 2006), which contrasts with the overall decrease driven by *A. lusitanicus*.

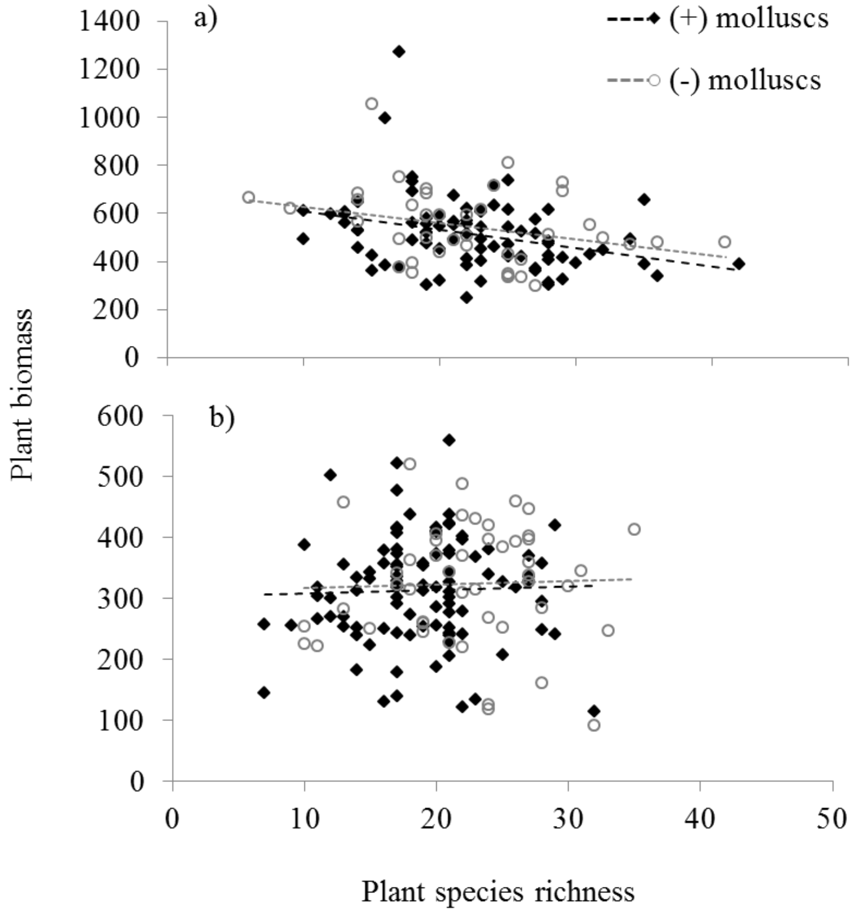

Figure 7. Plant species richness and biomass relationship in (+) and (-) mollusc plots in the years a) 2008 and b) 2009

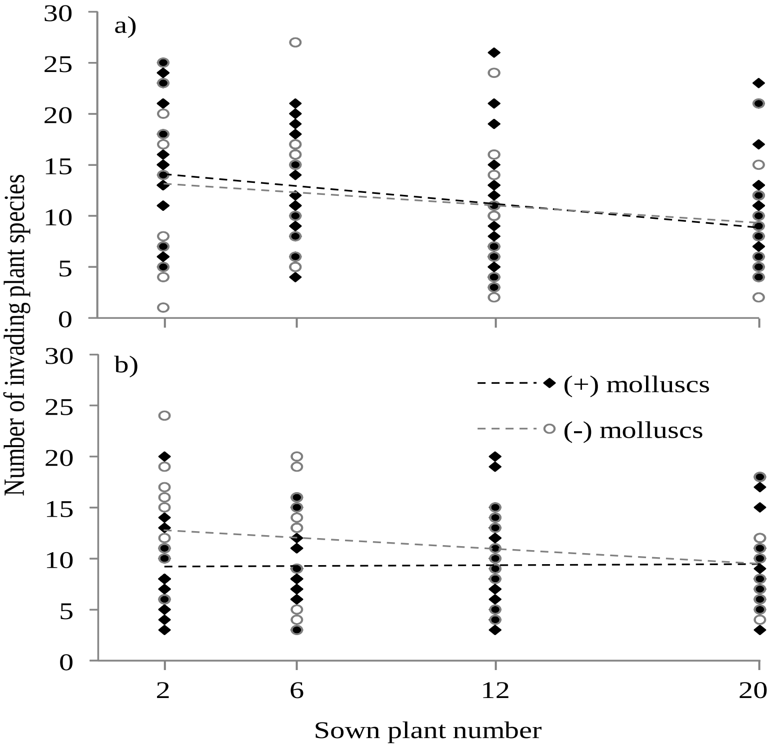

Figure 8. Invading and sown plant relationship in (+) and (-) mollusc plots in the years a) 2008 and b) 2009.

The plant functional groups had differential effects on the abundance of the slug species; however, the relationship between slug abundance and the cover or diversity of tall herbs, small herbs, legumes and grasses was, with one exception, always negative. Other studies on generalist herbivores have similarly shown that plant functional identity was more important than plant diversity in determining the level of herbivory by grasshoppers (Pfisterer *et al.* 2003; Scherber *et al.* 2010b) and soil fauna (Birkhofer *et al.* 2011) in grasslands. These findings are supported by the variation partitioning analysis: we found that a large fraction of the variation remained unexplained, which can be expected for such eurytopic species; however, plant composition was significantly related to the distribution of slug communities, and accounted for by far the greatest exclusive fraction of the explained variation. Plant composition can thus have a substantial effect on so-called generalist herbivores (Scherber *et al.* 2010b).

Vegetation height and plant biomass were, in general, positively correlated with the abundance of molluscs, supporting the plant architecture hypothesis (Lawton 1983). There was also a positive effect of plant biomass, but not of species richness, on the abundance of slug eggs. It suggests that vegetation structure and especially biomass is important for slugs when choosing egg-laying sites. The importance of vegetation structure on mollusc abundance has been shown for wetlands (Horsak *et al.* 2011), but rarely in agro-ecosystems within intensive agriculture (but see Dedov *et al.* 2006).

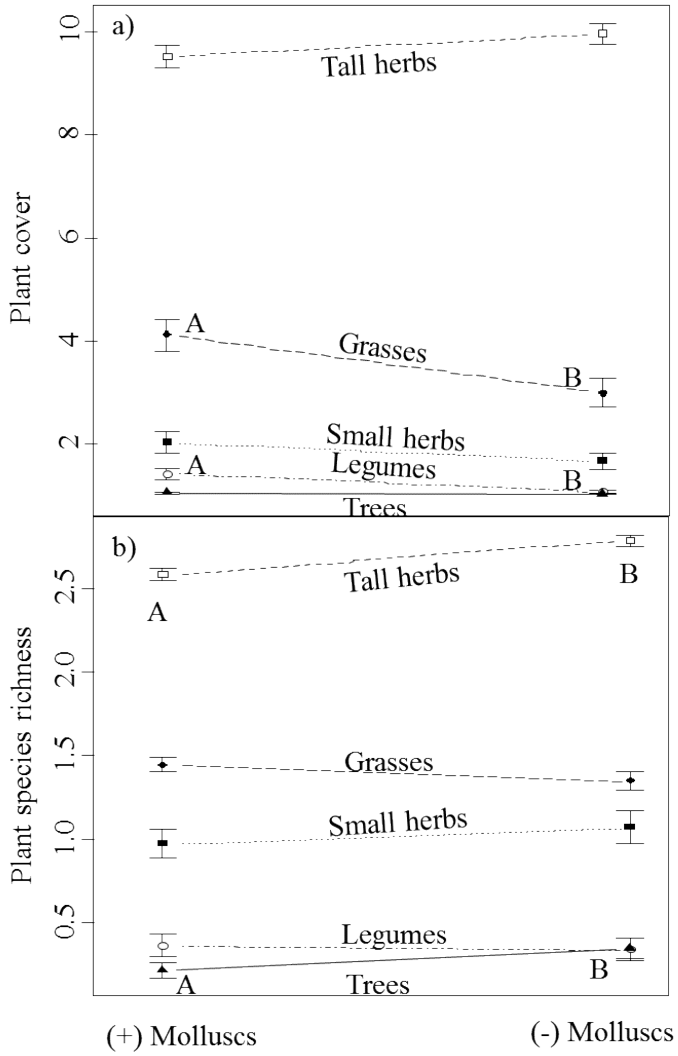

Figure 9. The effect of molluscs in the year 2009 on a) plant cover (in %, square root transformed), and b) plant species richness of five functional plant groups. Significant differences ($P < 0.05$) between treatments are represented by different letters. Symbols represent the means; error bars show the standard error.

Our treatment reducing the abundance of molluscs (predominantly the large species *A. lusitanicus*) revealed a substantial impact of slugs on the species richness and composition of wildflower strips after only two years. Total productivity, measured by biomass, was however not affected. Plant species richness was substantially greater when molluscs were reduced, which is in line with the finding that the establishment of invading plants was hindered in (+) mollusc plots. Specifically, there were more species of tall herbs and tree seedlings in (-) mollusc plots, at the expense of grass and legume cover, which is in accordance with other diversity studies (Allan & Crawley 2011) and feeding experiments using *A. lusitanicus* (Briner & Frank 1998) and *D. reticulatum* (Keller *et al.* 1999; Hensgen *et al.* 2011). For instance, *A. lusitanicus* shows clear preferences for annual plant species that are sown in wildflower strips and in crop fields over naturally occurring legumes and grasses (Briner & Frank 1998). Thus, these unpalatable plants occupy empty niches created by selective mollusc herbivory on certain tall herb species, a phenomenon that has been documented not only for molluscs in grassland (Allan & Crawley 2011), but also for grasshoppers (Scherber *et al.* 2010b). In the (+) mollusc plots, we found a higher abundance of *Dipsacus fullonum, Equisetum arvense*, *Trifolium repens, Lolium perenne* and *Dactylus glomerata*. Our findings for these species are supported by feeding (Hanley *et al.* 1995) and grassland experiments (Allan and Crawley 2011), providing evidence that they occupy empty niches produced by slug grazing on specific tall herbs.

A very encouraging result for farmers is the strong negative effect of mollusc grazing on *Cirsium arvense*, an agricultural pest plant that requires expensive and time-consuming herbicide control (Marshall *et al.* 2003; Ziska *et al.* 2004) and that can become abundant in wildflower strips. *Cirsium* is known to be affected by mollusc grazing in feeding experiments (Briner & Frank 1998), and we indeed found that *Cirsium* can be significantly reduced by slug herbivory despite a high availability of other palatable herbs.

Long-term field experiments in perennial grassland have yielded highly variable results, with examples in which there is no effect of aboveground herbivores on plant diversity or biomass (Stein *et al.* 2010), where there is negative effect of molluscs on plant diversity but a positive effect on plant biomass (Allan & Crawley 2011), or *vice versa* (Buschmann *et al.* 2005). This highlights the importance of performing long-term diversity experiments in the specific natural environments under concern, to draw conclusions about herbivore effects and conservation aspects.

Experimental caveats

The desired effect of the 8 mm fencing treatment was to decrease the abundance of major herbivores in the system, namely slugs and small rodents (common voles and wood mice). As in other field experiments, the exclusion of any trophic group is likely to be incomplete (Stein *et al.* 2010) even when pesticides, as in our study, are applied frequently at high dosage, or exclusion constructions are carefully built. As mentioned in the Methods, in the same 12 study strips, Meyer (2011) found more rodents in (-) mollusc compared to (+) mollusc plots (average ± s.d.: 2.1 ± 1.5 and 1.5 ± 1.2 captured rodents per plot, respectively). We can assume that this small numerical difference in rodent abundance had at most a minor contribution to the observed differences in vegetation. In contrast, there were much greater differences in mollusc abundances between (-) and (+) mollusc plots (average ± s.d.: 4.4 ± 2.1 and 18.4 ± 4.3 captured individuals, respectively). Moreover, the difference was most marked for the largest species, *A. lusitanicus*. Thus we suggest that the major vegetation differences between mollusc treatments derived from mollusc grazing. Pellet analyses showed that the common vole and the wood mouse have contrasting food preferences to molluscs; they prefer grasses and legumes (Lantova & Lanta 2009; Meyer 2011). Thus, the observed decrease in cover of both functional groups in the (-) mollusc plots may be partly attributed to an increased grazing pressure from rodents, reinforced by stronger competition with tall herbs released from herbivory by slugs.

In order to avoid disturbance to the plants, we did not search the vegetation exhaustively for molluscs or carry out soil sampling, which are considered the most reliable methods for mollusc sampling (South 1964). Surface trapping using tiles has limitations and does not estimate absolute abundances. Moreover, it shows a bias for slugs with higher body mass (Archard *et al.* 2004; Cordoba *et al.* 2011). However, the method is fully adequate to estimate differences in slug abundances between subplots and it enabled us to monitor the mollusc community development over a period of three years, without drastically reducing abundances as would have been the case had pitfall traps been used.

During the three years of the experiment, ants increasingly established colonies underneath the tiles. At the end of the experiment in autumn 2009, 57 out of 168 tiles (35%) were colonized by *Lasius niger* (Linnaeus 1758) and 2 tiles by *Lasius flavus* (Fabricius 1782). We found a positive effect of plant species richness and especially of legume, tall herb and small herbs on ant abundance (*lme* value = 0.05; P = 0.005, *unpublished data*). This effect can be expected, since a higher diversity of plants provides a higher diversity of resources in the form of aphids and seeds (Boulton *et al.* 2005; Scherber *et al.* 2010a; Haddad *et al.* 2011). Ant abundance was strongly negatively correlated with slug abundance, and in particular for *A. lusitanicus*. For this reason, ant abundance was accounted for in our analyses; we also reanalysed the data excluding all tiles with ants, which did not yield different results. Thus we can assume that ants do not mediate the effect of plant diversity on slug abundance. Surprisingly, (-) mollusc plots had significantly fewer ants than (+) mollusc plots. The application of molluscicide and/or vegetation effects could explain this negative impact on ants.

CONCLUSION

Our diversity experiment showed that plant diversity, structure and composition can have substantial effects on mollusc abundance and composition. In particular, the agricultural pest species Arion lusitanicus was less abundant in more diverse habitats. Species rich communities thus appear to be more resistant against generalist herbivores, as has been suggested for specialist herbivores by the resource concentration hypothesis (Root 1973). Plant species composition was the most important determinant of the overall composition of the gastropod community. This finding was supported by the differential effect of the five plant functional groups. Thus selective feeding and active habitat choice in molluscs might be the reason for lower abundances in diverse habitat patches. It should therefore be possible to optimize the species composition of wildflower strips to reduce their attractiveness to slugs, while maintaining their role in the promotion of ecosystem services such as pollination and the preservation of biodiversity in farmland.

We also provide evidence for a significant decrease in plant species richness caused by molluscs, resulting in a compositional change of the vegetation. Future studies on ecosystem functioning should therefore avoid focusing only on singular descriptors of vegetation, such as simple diversity or biomass, but in addition measure vegetation composition components and species traits. Also, the negative impact of slugs was evident only after two years; thus, to show the combined effect of herbivory and plant species richness on biomass, future studies might have to run for longer time.

Our results highlight the importance of differentiating the effects of plant diversity and composition on different herbivore species in ecosystem functioning research. They also demonstrate the protective role of plant biodiversity against generalist herbivores, which can in turn negatively impact plant diversity on a longer term, driving the system along a "low plant diversity – high mollusc abundance" trajectory.

ACKNOWLEDGEMENTS

We thank Jacques Studer and the farmers for their help in the realisation of this project. David Frey and Till Sander helped in the field and laboratory and François Meyer provided data about rodent abundances. Bernhard Seifert confirmed the determination of the ant species. We are grateful to two anonymous reviewers for their suggestions. This study was funded by the Swiss National Foundation and by the Fonds de la recherche de l'Université de Fribourg, Switzerland. The experiment complies with current Swiss laws.

APPENDIX

Table S1. Wildflower species composition and abundances. Internal = sown plants from the Swiss midland wildflower mixture. External = other species that were found in the experimental wildflower strips. Functional groups: TalH= tall herbs; SmlH= small herbs; Leg= legumes, SmlT= small trees and Grass= grasses. The numbers of plots the plant occurred in and the mean cover (%) are given for the years 2007, 2008 and 2009. Internal plant species in grey were not used in the fence experiments. All 24 internal plant species were used in the conventional wildflower mixture plots.

Plant species	Internal or External	Functional group	Number of plots in 2007	Number of plots in 2008	Number of plots in 2009	Mean cover 2007	Mean cover 2008	Mean cover 2009
Achillea millefolium L.	Int	TalH	96	120	113	3.367	6.750	4.442
Agrostemma githago L.	Int	TalH	76	24	16	3.239	0.199	0.015
Anthemis tinctoria L.	Int	TalH	83	100	98	3.956	6.405	6.419
Centaurea cyanus L.	Int	TalH	91	10	0	7.999	0.110	0.000
Centaurea jacea L.	Int	TalH	99	118	116	6.592	9.769	14.398
Cichorium intybus L.	Int	TalH	101	113	59	18.671	17.577	1.048
Daucus carota L.	Int	TalH	107	121	79	9.570	6.812	1.098
Dipsacus fullonum L.	Int	TalH	96	117	140	8.568	11.141	19.328
Echium vulgare L.	Int	TalH	88	105	53	7.584	6.263	0.297
Fagopyrum esculentum Moench	Int	SmlH	19	3	0	0.610	0.000	0.000
Hypericum perforatum L.	Int	TalH	47	94	96	0.242	1.362	3.033
Legusia speculum-veneris (L.) Chaix	Int	SmlH	10	0	0	0.036	0.000	0.000
Leucanthemum vulgare Lam.	Int	TalH	86	95	90	2.631	5.846	7.051
Malva moschata L.	Int	TalH	87	99	111	3.335	3.738	4.864
Malva sylvestris L.	Int	TalH	103	97	64	3.782	1.661	0.837
Melilotus albus Medik.	Int	Leg	20	24	20	0.115	0.051	0.788
Onobrychis viciifolia Scop.	Int	Leg	11	10	7	0.085	0.064	0.020
Origanum vulgare L.	Int	TalH	68	98	108	0.557	2.353	7.642
Papaver rhoeas L.	Int	TalH	90	40	16	0.908	0.400	0.173
Pastinaca sativa L.	Int	TalH	40	51	75	0.182	0.798	1.486
Silene latifolia Poir.	Int	TalH	90	117	108	1.765	3.410	2.242
Tanacetum vulgare L.	Int	TalH	96	109	106	2.172	4.000	6.079
Verbascum lychnitis L.	Int	TalH	45	65	90	0.532	1.180	1.898
Verbascum thapsus L.	Int	TalH	77	91	61	1.963	1.603	0.514
Acer pseudoplatanus L.	Ext	SmlT	1	5	6	0.000	0.000	0.001
Aethusa cynapium L.	Ext	TalH	21	23	0	0.069	0.207	0.000
Agrostis stolonifera L.	Ext	Grass	0	47	0	0.000	0.783	0.000
Althea officinalis L.	Ext	TalH	1	0	3	0.000	0.000	0.000
Amaranthus lividus L.	Ext	TalH	20	0	0	0.028	0.000	0.000
Amaranthus retroflexus L.	Ext	TalH	99	10	0	0.592	0.007	0.000
Anagallis arvensis L.	Ext	SmlH	71	35	10	0.327	0.224	0.003
Apera spica-venti (L.) Beauv.	Ext	Grass	9	1	68	0.007	0.051	1.880
Arrhenatherum elatius (L.) Beauv.	Ext	Grass	2	8	43	0.009	0.135	2.603
Borago officinalis L.	Ext	TalH	0	0	4	0.000	0.000	0.000
Brassica sp.1	Ext	TalH	1	0	0	0.001	0.000	0.000
Brassica sp.2	Ext	TalH	9	0	0	0.082	0.000	0.000
Brassica napus L.	Ext	TalH	33	1	0	0.413	0.000	0.000

Plant species	Internal or External	Functional group	Number of plots in 2007	Number of plots in 2008	Number of plots in 2009	Mean cover 2007	Mean cover 2008	Mean cover 2009
Bromus sp.	Ext	Grass	4	0	0	0.027	0.000	0.000
Campanula patula L.	Ext	TalH	0	1	0	0.000	0.019	0.000
Capsella bursa-pastoris (L.) Medik.	Ext	SmlH	107	12	0	1.019	0.028	0.000
Cardamine pratensis L.	Ext	TalH	0	0	5	0.000	0.000	0.006
Centaurium erythraea Rafn	Ext	SmlH	0	0	1	0.000	0.000	0.000
Cerastium sp.	Ext	SmlH	22	22	5	0.120	0.117	0.003
Chamomilla suaveolens	Ext	TalH	69	0	0	1.596	0.000	0.000
Chaenorhinum minus (L.) Lange	Ext	SmlH	18	8	0	0.018	0.015	0.000
Chamomilla recutita (L.) Rauschert	Ext	TalH	41	17	3	0.177	0.058	0.001
Chenopodium album L.	Ext	TalH	106	23	8	1.089	0.718	0.046
Chenopodium polyspermum L.	Ext	TalH	106	18	5	3.464	0.378	0.001
Chenopodium sp.	Ext	TalH	26	23	13	0.075	2.469	0.103
Circea lutetiana L.	Ext	SmlH	22	33	41	0.278	0.540	1.474
Cirsium arvense (L.) Scop.	Ext	TalH	0	0	1	0.000	0.000	0.001
Cirsium vulgare (Savi) Ten	Ext	TalH	0	0	3	0.000	0.000	0.000
Clematis vitalba L.	Ext	SmlH	0	0	1	0.000	0.000	0.000
Convolvulus arvensis L.	Ext	SmlH	5	13	16	0.003	0.116	0.125
Conyza canadensis (L.) Cronquist	Ext	TalH	0	29	54	0.000	0.327	1.200
Cornus sanguinea L.	Ext	TalH	3	0	15	0.000	0.000	0.046
Coronilla sp.	Ext	Leg	0	0	1	0.000	0.000	0.006
Crepis biennis L.	Ext	TalH	1	3	1	0.000	0.000	0.000
Dactylis glomerata L.	Ext	Grass	11	27	75	0.038	0.276	1.904
Deschampsia flexuosa (L.) Trin	Ext	Grass	0	0	3	0.000	0.000	0.115
Digitaria sanguinalis (L.) Scop.	Ext	Grass	2	3	0	0.024	0.000	0.000
Echinochloa crus-galli (L.) Beauv.	Ext	Grass	119	71	27	6.044	1.726	0.027
Elymus repens (L.) Gould	Ext	Grass	7	51	95	0.050	1.481	5.936
Epilobium hirsutum L.	Ext	TalH	0	0	3	0.000	0.000	0.000
Epilobium sp.1	Ext	TalH	21	100	93	0.014	0.821	3.356
Epilobium sp.2	Ext	TalH	0	0	91	0.000	0.000	3.479
Equisetum arvense L.	Ext	Grass	29	24	24	1.229	0.882	0.463
Erigeron annuus (L.) Pers.	Ext	TalH	0	1	8	0.000	0.000	0.000
Euphorbia amygdaloides L.	Ext	TalH	1	0	0	0.000	0.000	0.000
Euphorbia exigua L.	Ext	SmlH	3	0	0	0.002	0.000	0.000
Euphorbia helioscopia L.	Ext	TalH	6	10	4	0.010	0.021	0.000
Euphorbia stricta L.	Ext	TalH	0	13	1	0.000	0.169	0.000
Fallopia convolvulus (L.) A. Löwe	Ext	SmlH	2	33	8	0.002	0.149	0.007
Festuca sp.	Ext	Grass	0	2	10	0.000	0.001	0.154
Filaginella uliginosa (L.) Opiz	Ext	SmlH	19	6	0	0.047	0.008	0.000
Fragaria sp.	Ext	SmlH	0	1	0	0.000	0.000	0.000
Galinsoga ciliata (Raf.) S.F.Blake	Ext	SmlH	16	3	0	0.087	0.000	0.000
Galium album Miller	Ext	TalH	0	5	9	0.000	0.001	0.032
Galium aparine L.	Ext	SmlH	25	14	15	0.147	0.035	0.015
Geranium dissectum L.	Ext	SmlH	4	0	0	0.001	0.000	0.000
Geranium rotundifolium L.	Ext	SmlH	3	11	9	0.009	0.046	0.014
Geum urbanum L.	Ext	TalH	0	0	5	0.000	0.000	0.000

Plant species	Internal or External	Func-tional group	Number of plots in 2007	Number of plots in 2008	Number of plots in 2009	Mean cover 2007	Mean cover 2008	Mean cover 2009
Glechoma hederacea L.	Ext	SmlH	3	6	7	0.001	0.001	0.128
Grass sp.2	Ext	Grass	9	0	0	0.052	0.000	0.000
Grass sp.3	Ext	Grass	5	0	0	0.019	0.000	0.000
Grass sp.4	Ext	Grass	2	0	0	0.002	0.000	0.000
Grass sp.1	Ext	Grass	0	4	0	0.000	0.218	0.000
Gypsophila muralis L.	Ext	SmlH	2	0	0	0.000	0.000	0.000
Helianthus annuus L.	Ext	TalH	11	0	0	0.106	0.000	0.000
Holcus lanatus L.	Ext	Grass	3	17	58	0.010	0.192	1.630
Hypochoeris radicata L.	Ext	TalH	0	0	2	0.000	0.000	0.020
Juglans regia L.	Ext	SmlT	5	20	25	0.001	0.014	0.083
Juncus bufonius L.	Ext	Grass	19	4	5	0.137	0.032	0.000
Juncus sp.	Ext	Grass	2	4	4	0.002	0.032	0.019
Kickxia elatine (L.) Dumort.	Ext	SmlH	25	2	0	0.961	0.006	0.000
Kickxia spuria (L.) Dumort.	Ext	SmlH	18	13	7	0.038	0.226	0.038
Lactuca serriola L.	Ext	TalH	0	11	7	0.000	0.372	0.424
Lamiaceae	Ext	SmlH	1	0	0	0.000	0.000	0.000
Lamium amplexicaule L.	Ext	SmlH	0	2	2	0.000	0.001	0.000
Lamium purpureum L.	Ext	SmlH	18	17	6	0.009	0.005	0.000
Linaria vulgaris L.	Ext	SmlH	11	17	22	0.023	0.142	0.629
Lolium perenne L.	Ext	Grass	18	71	67	0.273	0.938	2.540
Lotus corniculatus L.	Ext	Leg	23	10	16	0.175	0.001	0.013
Lythrum salicaria L.	Ext	TalH	0	0	5	0.000	0.000	0.000
Malva neglecta Wallroth	Ext	TalH	2	0	0	0.008	0.000	0.000
Medicago lupulina L.	Ext	Leg	3	5	2	0.002	0.001	0.001
Medicago sativa L.	Ext	Leg	0	1	2	0.000	0.000	0.000
Mentha arvensis L.	Ext	SmlH	0	3	3	0.000	0.058	0.045
Mercurialis annua L.	Ext	TalH	26	12	5	0.253	0.016	0.039
Myosotis arvensis (L.) Hill	Ext	SmlH	13	10	8	0.008	0.003	0.007
Oenothera biennis L.	Ext	TalH	0	1	1	0.000	0.000	0.000
Orobanche sp.	Ext	SmlH	0	3	2	0.000	0.000	0.001
Oxalis stricta L.	Ext	SmlH	20	34	12	0.057	0.113	0.188
Phacelia tanacetifolia Benth.	Ext	TalH	2	0	0	0.008	0.000	0.000
Phleum pratense agg.	Ext	Grass	6	12	17	0.012	0.045	0.346
Phragmites australis (Cav.) Trin	Ext	Grass	0	0	1	0.000	0.000	0.000
Plantago lanceolata L.	Ext	SmlH	15	25	22	0.076	0.180	0.263
Plantago major L.	Ext	SmlH	101	111	37	1.543	1.398	0.284
Poa annua L.	Ext	Grass	91	27	3	1.775	0.457	0.051
Polygonum aviculare L.	Ext	SmlH	27	42	9	0.156	1.106	0.021
Polygonum mite Schrank	Ext	TalH	33	26	6	0.372	0.123	0.001
Polygonum sp.	Ext	TalH	36	5	0	0.571	0.001	0.000
Populus alba L.	Ext	SmlT	0	0	3	0.000	0.000	0.000
Portulaca oleracea L.	Ext	SmlT	2	0	0	0.002	0.000	0.000
Potentilla reptans L.	Ext	SmlH	2	4	6	0.000	0.006	0.007
Prunella vulgaris L.	Ext	SmlH	0	4	1	0.000	0.000	0.000
Ranunculus repens L.	Ext	SmlH	5	22	17	0.074	0.250	0.084

Plant species	Internal or External	Func-tional group	Number of plots in 2007	Number of plots in 2008	Number of plots in 2009	Mean cover 2007	Mean cover 2008	Mean cover 2009
Rubus sp.	Ext	SmlH	10	7	11	0.068	0.000	1.032
Rumex obtusifolius L.	Ext	TalH	68	65	77	1.108	0.692	1.327
Rumex sp.	Ext	TalH	4	0	0	0.000	0.000	0.000
Sagina apetala Ard.	Ext	SmlH	1	1	0	0.000	0.000	0.000
Salix alba L.	Ext	SmlT	2	8	26	0.000	0.007	0.007
Salix caprea L.	Ext	SmlT	0	1	4	0.000	0.000	0.000
Scrophularia nodosa L.	Ext	TalH	2	1	6	0.000	0.000	0.001
Senecio vulgaris L.	Ext	TalH	25	19	0	0.055	0.001	0.000
Setaria pumila (Poir.) Schult.	Ext	Grass	36	46	25	0.781	0.698	0.359
Sinapis alba L.	Ext	TalH	0	1	0	0.000	0.000	0.000
Solanum canadensis	Ext	TalH	0	0	2	0.000	0.000	0.000
Solanum nigrum L.	Ext	SmlH	46	9	1	0.379	0.000	0.000
Sonchus arvensis L.	Ext	TalH	80	69	0	0.503	0.893	0.000
Sonchus asper (L.) Hill	Ext	TalH	0	15	35	0.000	0.090	0.242
Sonchus oleraceus L.	Ext	TalH	12	10	2	0.029	0.026	0.000
Stellaria media (L.) Vill.	Ext	SmlH	104	60	17	2.340	0.691	0.018
Taraxacum officinale Wigg	Ext	SmlH	66	67	51	2.429	1.051	1.228
Taraxacum sp.	Ext	SmlH	1	0	1	0.032	0.000	0.000
Thlaspi arvense L.	Ext	SmlH	4	0	0	0.009	0.000	0.000
Trifolium arvense L.	Ext	Leg	1	0	0	0.000	0.000	0.000
Trifolium campestre Schreb	Ext	Leg	2	0	0	0.009	0.000	0.000
Trifolium sp.1	Ext	Leg	2	0	0	0.000	0.000	0.000
Trifolium pratense L.	Ext	Leg	19	28	11	0.106	0.469	0.026
Trifolium repens L.	Ext	Leg	72	60	36	1.163	0.841	0.342
Trifolium sp.2	Ext	Leg	1	0	1	0.001	0.000	0.006
Tripleurospermum inodorum L.	Ext	TalH	4	0	4	0.017	0.000	0.026
Triticum sp.	Ext	Grass	9	18	12	0.028	0.032	0.000
Urtica dioica L.	Ext	TalH	1	5	5	0.000	0.000	0.000
Veronica verna L.	Ext	SmlH	5	0	0	0.003	0.000	0.000
Verbena officinalis L.	Ext	TalH	0	5	14	0.000	0.006	0.026
Veronica persica Poir.	Ext	SmlH	94	58	37	2.292	0.173	0.053
Veronica serpyllifolia L.	Ext	SmlH	4	4	1	0.000	0.007	0.000
Vicia hirsuta (L.) Gray	Ext	Leg	6	5	5	0.009	0.000	0.013
Vicia sativa L.	Ext	Leg	7	0	2	0.011	0.000	0.000
Viola arvensis Murray	Ext	SmlH	17	18	6	0.119	0.021	0.001

Table S2. Body mass analysis of the three most abundant mollusc species
Significance levels at: † P < 0.1, * P < 0.05, ** P < 0.01 and *** P < 0.001

Linear mixed-effects model fit by maximum likelihood for slug body mass

Fixed effects:
treatment + plant species richness + effective number of species + biomass + veg. height + year + season

Data: *Arion lusitanicus*

Random effects: Formula: ~1 |wildflower strip

	Intercept	Residuals
s.d.:	3.71	9.75

Fixed effects:	Value	Std.Error	DF	t-value	p-value	
Intercept	26.83	4.97	211	5.40	0.000	
25 mm fence	1.06	1.45	211	0.73	0.467	
8 mm fence	-1.86	2.01	211	-0.93	0.356	
Plant species richness	1.10	0.75	211	1.47	0.143	
Effective number of species	-0.67	0.92	211	-0.73	0.468	
Plant Biomass	3.44	1.03	211	3.33	0.001	**
Vegetation height	-0.19	0.87	211	-0.22	0.826	
Year 2008	-3.01	5.06	211	-0.59	0.553	
Year 2009	-8.12	4.83	211	-1.68	0.094	†
Season spring	-11.43	1.81	211	-6.33	<0.001	***

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-2.60	-0.49	-0.12	0.35	5.57

Number of Observations: 232
Number of Groups: 12

Table S3. continued

Data: *Deroceras reticulatum*

Random effects: Formula: ~1 |wildflower strip

	Intercept	Residuals
s.d.:	0.19	0.84

Fixed effects:	Value	Std.Error	DF	t-value	p-value	
(Intercept)	1.61	0.18	245	9.12	0.000	
25 mm fence	-0.12	0.13	245	-0.93	0.352	
8 mm fence	0.00	0.14	245	0.01	0.992	
Plant species richness	0.03	0.07	245	0.42	0.678	
Effective number of species	0.01	0.07	245	0.16	0.876	
Plant biomass	0.03	0.09	245	0.32	0.746	
Vegetation height	-0.08	0.08	245	-1.02	0.308	
Year 2008	-0.77	0.22	245	-3.53	0.001	**
Year 2009	-0.40	0.20	245	-1.99	0.048	*
Season spring	0.00	0.18	245	-0.03	0.980	

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.62	-0.57	-0.11	0.33	6.70

Number of Observations: 266
Number of Groups: 12

Data: *Deroceras panormitanum*

Random effects: Formula: ~1 |wildflower strip

	Intercept	Residuals
s.d.:	0.12	0.45

Fixed effects:	Value	Std.Error	DF	t-value	p-value	
(Intercept)	0.68	0.14	137	4.70	0.000	
25 mm fence	0.03	0.09	137	0.39	0.701	
8 mm fence	-0.14	0.10	137	-1.32	0.188	
Plant species richness	-0.03	0.05	137	-0.63	0.533	
Effective number of species	0.03	0.04	137	0.66	0.509	
Plant biomass	-0.04	0.06	137	-0.66	0.510	
Vegetation height	0.03	0.06	137	0.56	0.579	
Year 2008	-0.28	0.17	137	-1.69	0.094	†
Year 2009	0.23	0.15	137	1.52	0.131	
Season spring	-0.31	0.19	137	-1.62	0.107	

Standardized Within-Group Residuals:

Min	Q1	Med	Q3	Max
-1.86	-0.64	-0.09	0.371	4.80

Number of Observations: 158
Number of Groups: 12

Table S4. Total mollusc abundance in relation to the meteorological data. Parameters of Generalized linear mixed effect models with a correlation structure between sessions and the traps within the wildflower strips. Significance levels at: † P < 0.1, * P < 0.05, ** P < 0.01 and *** P < 0.001

	Air temperature (°C)	Optimum air temperature $(°C)^2$	Air humidity (%)	Optimum air humidity $(\%)^2$
Molluscs	-0.329	0.000	1.274 **	-1.466 ***
Arion lusitanicus	-0.199	0.355	0.471 †	-0.414 †
Deroceras reticulatum	-0.277	-0.091	0.857 *	-1.008 **
Deroceras panomitanum	-0.034	0.026	0.024	-0.025

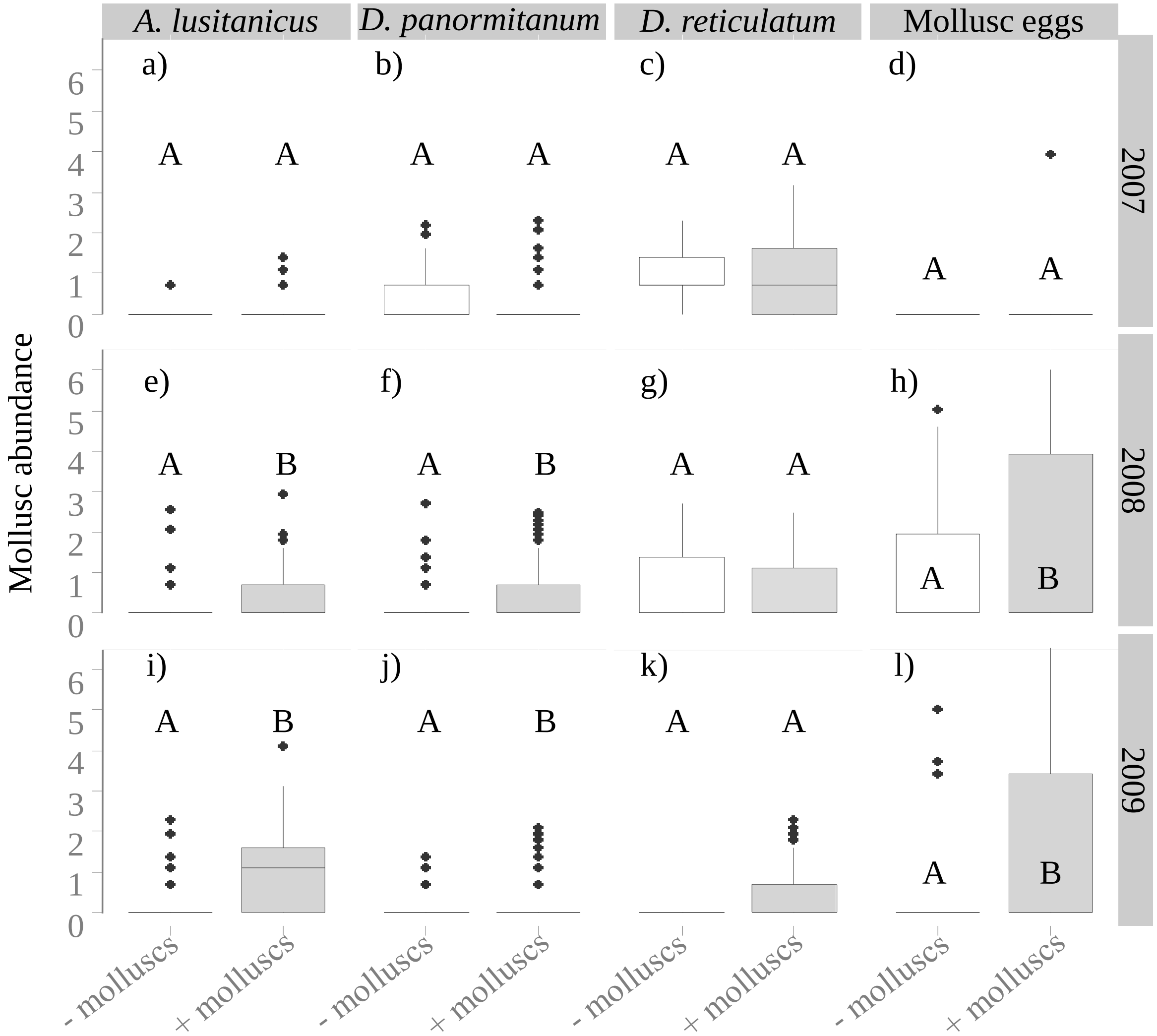

Figure S1. Abundances of the molluscs *A. lusitanicus*, *D. panormitanum*, *D. reticulatum* and mollusc egg abundance (left to right) in 2007, 2008 and 2009 (top to bottom) in the mollusc treatments (- white and + grey). The twelve graphs a) - l) show logarithmic means (of two seasons and twelve wildflower strips) of slug abundances for each of the three species and the mollusc eggs. Different letters A-B show significantly different slug abundances ($P < 0.05$) within one species, between the mollusc treatments in the corresponding year analysed by linear mixed effect models. The box plots represent the median, the upper and lower borders of the boxes 25 and 75 quartiles and lines give the maximum and minimum. Dots indicate abundances that are considered as outliers.

Chapter 3

Plant diversity in a nutshell: testing for small-scale effects on trap nesting wild bees and wasps

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Submitted to Ecosphere

ABSTRACT

Declining plant species richness in agro-ecosystems and thus reduced habitat quality can have cascading effects on ecosystem functioning, leading to reduced pollination and biological control. Here we test if plant diversity can affect arthropod diversity and abundance on a very small scale, manipulating plant species richness (2, 6, 12 and 20 sown species) in small subplots (6 by 9 meters) in wildflower strips in an agricultural landscape. We simultaneously analyzed the effect of plant species richness, vegetation structure, and plant composition on the species richness and abundance of cavity-nesting wild bees, wasps, their prey and natural enemies, and on the structure of their food webs. By separating the trap-nesting species into functional groups according to their prey, we aimed to understand the underlying patterns for the effects of plant diversity. Increasing plant species richness resulted in higher wasp species richness, with significantly greater abundance of spider-predating wasps. In turn, spider-predating wasp abundance negatively correlated with the abundance of spiders, suggesting top-down control. In contrast, bees and the food-web structure were unaffected by plant diversity. Interestingly, the abundance of spiders was the only variable that was strongly affected by plant composition, with models performing better when the correlation due to plant composition was included in the error structure. Our study showed that small-scale plant diversity loss can have surprising effects on cavity-nesting wasp diversity and abundance. Thus, preserving even small islands of plant diversity can contribute to the conservation of ecosystem services in agricultural landscapes.

Keywords: pollinators, biological control, *Trypoxylon figulus*, parasitism, quantitative food webs, plant composition, resource heterogeneity hypothesis

INTRODUCTION

Biodiversity loss due to intensification in agriculture is an important driver of reduced ecosystem functioning (Cardinale *et al.* 2006). Plant species richness has often been central to this discussion (Hooper *et al.* 2005) and has been identified as an important determinant of the diversity of consumers (Haddad *et al.* 2009; Scherber *et al.* 2010a). Two non-exclusive hypotheses have been formulated to explain the relationship between plant diversity and herbivore abundance and diversity. First, the *resource heterogeneity hypothesis* (Hutchinson 1959) argues that higher plant diversity offers greater resource heterogeneity, resulting in a higher diversity of consumers. Second the *more individuals hypothesis* (Srivastava & Lawton 1998) suggests that diverse plant communities are often more productive than simple plant communities (Tilman *et al.* 2001), and thus the greater quantity of resources available for consumers increases their abundance and diversity. Both hypotheses have found support in previous studies (Knops *et al.* 1999; Haddad *et al.* 2009).

At higher trophic levels, predator species may simply respond to increased diversity or productivity of resources provided by their prey in diverse plant communities (*resource heterogeneity* and *more individuals hypotheses* acting at the predator level), or they may respond positively to structural habitat diversity in diverse and productive plant communities. Consequently, plant diversity could alter the structure of associated animal communities, with top-down effects of predators limiting herbivore abundances in more diverse plant communities, as predicted by the *enemy hypothesis* (Root 1973). Thus declining plant species richness can have cascading effects and lead to reduced ecosystem functioning (Knops *et al.* 1999; Balvanera *et al.* 2006). The complexity of biotic interactions should decrease even faster than simple species diversity and abundance as plant diversity declines, and hence will leave systems more prone to further extinction (Tylianakis *et al.* 2008).

Quantitative food webs describing the feeding links and interaction strength among species can be used to explore the factors that structure and maintain ecological communities (Bersier, Banasek-Richter & Cattin 2002; Tylianakis, Tscharntke & Lewis 2007). Beyond the simple effects of extinction, changes in food-web structure due to human intervention may have important consequences for conservation and ecosystem functioning (Pimm 1979; McCann 2000).

In addition to plant species richness, the composition of the plant community can affect the species richness, abundance and food-web structure of consumers and higher trophic levels (Hooper & Vitousek 1997; Haddad *et al.* 2001; Viketoft *et al.* 2009; Scherber *et al.* 2010b). Usually, plant composition was analyzed separately from plant diversity and structure, either in a multivariate approach (Chapter 2), separated into functional group count (e.g. grasses, herbs, legumes) and composition (Hector *et al.* 1999; Haddad *et al.* 2009; Scherber *et al.* 2010b), or analyzed as dissimilarity matrixes in Mantel tests (Ebeling *et al.* 2012). To our knowledge, studies that simultaneously analyzed the effect of plant diversity, plant composition and structure on insect diversity and abundance and ultimately food-web structure are rare.

To counter species decline in agro-ecosystems, agri-environmental schemes have been introduced in Europe, aiming to increase the quality and abundance of agricultural compensation zones (Kleijn *et al.* 2009; Haaland, Naisbit & Bersier 2011). One element in these schemes is the establishment of wildflower strips, consisting of field margins or patches sown with a recommended plant mixture containing 24 herb species and maintained for six years (Nentwig 2000). The wildflower species mixture was elaborated in order to benefit a maximal number of different functional groups of animals for ecosystem services (Nentwig 1992; Pfiffner & Wyss 2003; Carvell *et al.* 2007).

Among those species likely to colonize wildflower strips, solitary cavity-nesting bees and wasps (Hymenoptera; Aculeata) provide valuable ecosystem services in agricultural landscapes (Gathmann & Tscharntke 1997). Easily studied using trap nests, they have been used to determine effects of ecological change (Holzschuh, Steffan-Dewenter & Tscharntke 2010), or habitat quality (Tscharntke, Gathmann & Steffan-Dewenter 1998; Albrecht *et al.* 2007; Sobek *et al.* 2009; Ebeling *et al.* 2012). Cavity-nesting bees act as pollinators and collect pollen or nectar as food for their larvae (Westrich 1989; Gathmann & Tscharntke 1999a). Cavity-nesting wasps can act as biological control agents by collecting herbivorous arthropods (Tscharntke, Gathmann & Steffan-Dewenter 1998), including phloem-sucking aphids (Aphididae), or larvae of smaller moths (microlepidoptera), leaf beetles (Chrysomelidae) and weevils (Curculionidae). Other species act as intraguild predators by feeding on spiders (Araneae), which themselves are beneficial as predators in agricultural ecosystems (Schmidt-Entling & Dobeli 2009). Thus, the wasps can easily be separated into three functional groups according to their trophic guilds, as predators of aphids, herbivores, or spiders. The abundance and species richness of trap-nesting bees and wasps may, either directly, through the availability of pollen and nectar sources, or indirectly, through the availability of their different prey taxa, be associated with vegetation composition, diversity and structure. In addition, although it is known that prey abundance has important effects on the abundance of predators (Volterra 1931; Cohen, Jonsson & Carpenter 2003), earlier studies on trap nests included plant species richness, but not specific prey abundances (e.g. Albrecht *et al.* 2007; Ebeling *et al.* 2012).

We used mixed effect models to simultaneously analyze the effect of plant composition, plant diversity and vegetation structure on the diversity and abundance of different functional groups and their food-web structure in trap nests in a plant diversity experiment within wildflower strips. We tested the following hypotheses:

(1) Plant diversity affects the diversity and abundance of bees, wasps and their enemies in trap nests according to the *resource heterogeneity* and *more individuals hypotheses*. These effects can be measured for some groups even on a very small scale.

(2) The strength of this effect differs among insect functional groups, decreasing with increasing trophic level in the following order: 1) bees, 2) herbivore- and aphid-predating wasps, 3) spider-predating wasps, and 4) enemies of trap-nesting bees and wasps.

(3) Interaction diversity within food webs decreases more rapidly with plant diversity loss than simple species richness.

METHODS

WILDFLOWER STRIP MANIPULATIONS

In spring (April-June) 2007 twelve wildflower strips were sown manually in fields around the village of Grandcour, 10 km south of Lake Neuchâtel in north-west Switzerland (479 m altitude; coordinates: 46° 52' N 06° 56' E). Annual average air temperatures are 10.1 °C and annual precipitation is approximately 941 mm in the region (Confederation 2011). The region is characterized by intensive agriculture embedded in a small-scale mosaic of arable fields, meadows and forests (Chapter 4).

The wildflower strips (hereafter strips) were each divided into three blocks of 216 m^2, which were randomly assigned to one of three trophic compositions: 1) control unfenced; 2) fenced with the aim of excluding slugs, micromammals and their main vertebrate predators; and 3) fenced to exclude only the vertebrate predators (as explained in detail in Chapter 2). These treatments did not affect the trap-nest community analyzed here (see statistical analysis below). Within each trophic treatment, four subplots (6 by 9 meters) differing in plant diversity (2, 6, 12, 20 sown species) were randomly assigned (Figure 1) and established from seeds of the conventional wildflower seed mixture (Günter 2000). The order and species composition of the plant diversity subplots was the same in the three fence treatments within a strip (Figure 1), but differed between strips. Thus, in total each of the 12 strips consisted of 12 subplots (3 fencing x 4 diversity treatments). In contrast to other biodiversity experiments (e.g., Cedar Creek, Tilman *et al.* (2001) and Jena Experiment, Roscher *et al.* (2004)), the plots were not weeded, so that the plant communities are the result of self-assemblage following initial sowing.

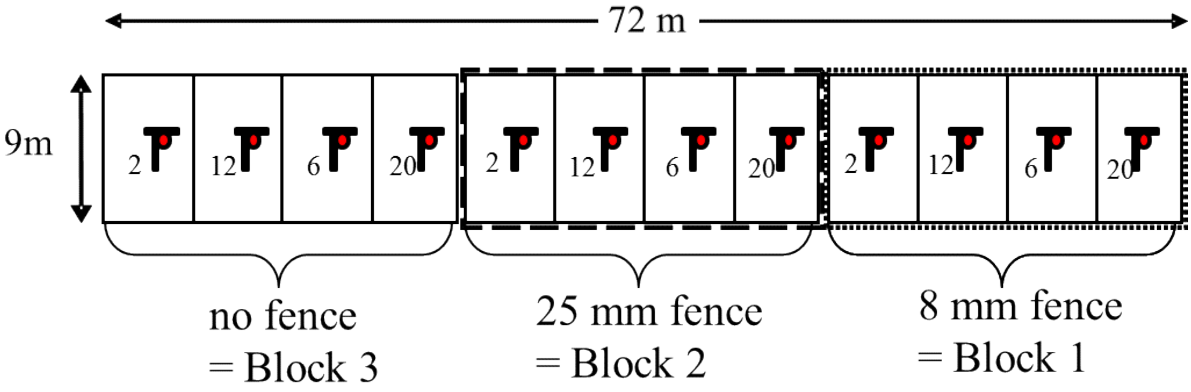

Figure 1. Experimental set up of 12 trap-nests (red circles) within subplots in wildflower strips. Numbers indicate sown plant species richness. Strips were divided into three blocks of equal size, with 3 fence treatments: 1) fence with 8 mm mesh (dotted-line), 2) fence with 25 mm mesh (dashed-line) and 3) no fence.

VEGETATION

Vegetation sampling took place in autumn 2008. *Plant diversity* was characterized by the total plant species richness and the percentage cover for each species was visually estimated using the standard method of Braun-Blanquet (Perner *et al.* 2005) for each subplot. The sown plant species number was positively correlated with the total plant species richness ($r = 0.13$, $df = 280$, $P = 0.014$). Vegetation structure was characterized by the average *vegetation height* and *plant biomass*. Average vegetation height was estimated visually at 10 cm resolution.

Plant biomass was assessed by measuring the leaf area index (LAI) with a LAI-2000 (LI-COR Biosciences) at 24 random points in each subplot in autumn 2008. The method was calibrated by cutting 5 biomass samples in 8 subplots, and the resulting linear relationship (Pearson product-moment correlation $r = 0.89$) was used to transform the average LAI values to plant biomass per subplot in dry weight g/m^2.

TRAP NESTS

Community composition. Trap nests enabled us to study species richness, abundance, and interactions of above ground nesting hymenopterans and their natural enemies under standardized nest site conditions (Tscharntke, Gathmann & Steffan-Dewenter 1998). Trap-nests consisted of 170 -180 twenty-cm long internodes of common reed *Phragmites australis*, placed in 20-cm long plastic pipes of 10 cm diameter. The diameters of reed internodes ranged from 2 to 10 mm. One trap was placed within each subplot, fixed at a height of 1.3 m on a wooden pole and protected by a 30 x 30 cm wood roof. After collection they were stored at 4°C for at least seven weeks to simulate winter. Twenty-seven nests were destroyed while in place, including nearly all of those in two strips, thus in total 117 trap nests from 10 strips were analyzed.

In spring 2009, all reed internodes containing nests were opened and counts made of the number of brood cells and the occurrence of (clepto-) parasites, parasitoids and predators (hereafter called “enemies”) attacking the nest-makers (hereafter called “hosts”). Nests were stored separately in glass tubes to collect emerging adults for identification. Individuals were identified using the following resources: Megachilidae, Amiet *et al.* (2007); Sphaecidae, De Beaumont (1964); Pompilidae, Wolf (1972); Eumenidae, Schmid-Egger (2004); Sapygidae, Amiet (2008); and Chrysididae, Bellmann (1995) and Linsenmaier (1997). Several specimens of each species were verified by taxonomists (see acknowledgements). If no adult emerged, features of the nest and larval food were used to identify the genus or (sub-) family based on Gathmann and Tscharntke (1999b). Empty brood cells of eumenid wasps were assumed to belong to the bivoltine *Ancistrocerus nigricornis*, since it was the only species for which offspring of the first generation emerged before trap collection (Krewenka *et al.* 2011).

Species richness and abundance (number of brood cells) in each subplot were recorded for the entire trap-nest community and separately for the following groups: pollen- and nectar-collecting bees (Apidae), all wasps and the functional groups: herbivore-predating wasps (Eumenidae and Sphecidae, feeding on Chrysomelidae, Curculionidae, Caelifera, and microlepidoptera larvae), aphid-predating wasps (Sphecidae of the genera *Passaloecus, Pemphredon,* and *Psenulus*), spider-predating wasps (Pompilidae and Sphecidae of the genus *Trypoxylon*), and enemies (see Table S1).

Food-web metrics. Quantitative host-enemy interaction food webs were constructed based on the pooled data from the three equal diversity subplots of each strip, and three quantitative food-web metrics were calculated following Bersier, Banasek-Richter and Cattin (2002), using the bipartite package (Dormann *et al.* 2009) in R (R Development Core Team 2012). *Vulnerability* is the weighted mean effective number of enemies per host species and *generality* is the weighted mean effective number of hosts per enemy species. *Interaction diversity* is a measure of the Shannon diversity of interactions that takes both the number and the evenness of interactions into account (Tylianakis, Tscharntke & Lewis 2007). For comparison, qualitative food-web metrics were calculated based on binary presence/absence interaction data. We analyzed three additional qualitative food-web metrics. *Connectance* is the proportion of links that are realized. *Nestedness* is a measure of departure from a systematic arrangement of species by niche width whereby the niches of more specialized species fall within those of more generalized species, ranging from 0 to 100, high to low nestedness (Atmar & Patterson 1993). The *number of compartments* is the number of subwebs within a web, where a subweb is a set of interconnected species with no links to members of other subwebs (Tylianakis, Tscharntke & Lewis 2007).

AVAILABILITY OF ARTHROPOD PREY

To estimate arthropod abundance in each subplot of the 10 strips, vacuum (hereafter D-vac) samples were taken in May 2008, between 10.00 and 16.00 on dry and sunny days. A foliage hoover type SH 85C (Stihl, Dieburg, Germany) was used to sample for two minutes from an area of 1 m^2 in the center of each of the 117 analyzed subplots (Figure 1). Collected arthropods were stored in ethanol and grouped into orders. Aphid (Aphidina) and spider (Araneae) abundances served as estimates of food availability for aphid- and spider-predating wasps, respectively. Total abundances of butterfly larvae (Lepidoptera), Psocoptera, beetle larvae (Coleoptera) and grasshoppers (Caelifera) per subplot (Table S3) served as estimates of food availability for herbivore-predating wasps. For the analysis of total wasp species richness and abundance, the summed abundance of all the above named groups was counted as “arthropods”.

STATISTICAL ANALYSES

All analyses were carried out using R version 2.12.0 (R Development Core Team 2012). To determine the best structure of the random factors, we first analyzed linear models with the response variables bee, wasp and enemy species richness and abundance and tested for differences between strips and between trophic treatment blocks. Models with only strips as random factor always performed best (lowest AIC; linear models difference between strips $P < 0.05$) compared to models with either trophic treatment (linear models difference between treatments $P > 0.05$), or strip and trophic treatment as random factors, thus we used the ten strips as random factors in all following analyses.

We analyzed the data using a linear mixed effect model with a correlation structure induced by the vegetation similarity between subplots. Our model is given by

$$y_{i,j} = \beta_0 + \beta_1(\log(S)_{i,j}) + \beta_2(Height)_{i,j} + \beta_3(Biomass)_{i,j} + \beta_4(Additional)_{i,j} + z_j + \varepsilon_{i,j} ,$$

where the indices *i* and *j* denote the subplot and the wildflower strip, respectively. As response variables ($y_{i,j}$), we tested: the species richness and number of brood cells of all trap nest species, hosts, enemies, bees, wasps, and the three wasp functional groups, and the abundance of spiders, aphids and herbivores from the D-vac samples. The following covariates were used: the natural logarithm of number of plant species ($\log(S)$), the average vegetation height (*Height*) and the average plant biomass (*Biomass*). As additional explanatory variables (*Additional*), we used: 1) the abundance of D-vac collected arthropods, spiders, herbivores and aphids, in the analysis of the abundance and species richness of all wasps, spider-, herbivore- and aphid-predating wasps, respectively; 2) the host species richness and number of brood cells in the analysis of enemy richness and number of parasitized cells, respectively; 3) the abundance of the respective predatory wasp group in the analysis of the abundance of D-vac collected aphids, spiders and herbivores; and 4) the abundance of D-vac collected spiders for aphids and herbivores, and of herbivores for spiders. The parameter β_0 denotes the intercept and $\beta_{1\text{-}4}$ denote the parameter estimates for the slopes on each variable. The ten wildflower strips were considered as random factors with $z_j \sim N(0, \sigma_z^2)$, where σ_z^2 denotes the random effect variance. The similarities in vegetation between subplots were included as correlation structure in the residuals. Specifically, we do not consider the residuals as independent (which is the usual assumption in linear models). In our model the correlation between the residuals from subplot (i_1,j_1) and (i_2,j_2) is proportional to their vegetation similarity measured as the Bray-Curtis index (Bray & Curtis 1957), i.e. $\varepsilon_{i,j} \sim N\left(0, \Sigma\right)$, where the elements of the variance-covariance matrix are given by

$$\Sigma_{(i_1,j_1),(i_2,j_2)} = \begin{cases} \sigma^2 & \text{if} \quad (i_1, j_1) = (i_2, j_2) \\ \sigma^2 \cdot \left(\text{Bray-Curtis}\right)_{(i_1,j_1),(i_2,j_2)} \cdot \lambda & \text{if} \quad (i_1, j_1) \neq (i_2, j_2). \end{cases}$$

The parameter λ, which ranges from 0 to 1, determines the strength of the correlation structure induced by the vegetation similarity. Note that for $\lambda = 0$, our model is simply equivalent to a standard linear mixed effect model. In order to determine if the correlation structure between the subplots induced by the plant composition was significant, we fitted models with and without inclusion of the correlation structure by maximum likelihood technique (see Chapter 9.2.4. in Davison 2003) and then we computed the AIC (Zuur *et al.* 2009). Finally, the parameters were estimated using the restricted maximum likelihood technique (REML, see Chapter 9.2.4. in Davison 2003). We examined Q-Q plots and Shapiro-Wilk tests of the normalized residuals of the models and Box-Cox transformed the response variables when necessary, to meet the assumptions of normality (Fox & Weisberg 2011). All continuous explanatory variables were scaled to zero mean and unit variance (Oksanen *et al.* 2011). The REML and ML codes can be provided upon request.

The food-web metrics (vulnerability, generality, interaction diversity, connectance, nestedness and number of compartments) were analyzed using the same procedure, with the explanatory variables: plant species richness (log), vegetation height, plant biomass and trap-nest species richness (to account for the possible dependence of the food-web metrics on the latter; Banasek-Richter *et al.* 2009).

The species composition of the entire community and of the four trophic guilds was analyzed with respect to 1) plant species richness and effective number of plant species (based on the Shannon diversity, see Jost 2006), vegetation height and biomass, and 2) vegetation composition of the 40 most abundant plant species over all strips, using constrained correspondence analyses (CCA) in *vegan* (Oksanen *et al.* 2011). Trap nest species with less than ten individuals were down-weighted; the effect of the strip identity was removed ("partialled out") as conditioning variable. The importance of the predictors was tested using the function *anova* with 9999 permutations. Plant species that significantly affected the composition of the trap nest community were identified using the function *ordistep* with backward stepwise model selection using 9999 permutations.

RESULTS

In total we recorded 13795 brood cells of 38 host species in the 117 trap nests. Bees were represented by 13 species in 9442 brood cells and wasps by 25 species in 3926 brood cells (Table S1). The most abundant bee species was the Red Mason bee, *Osmia bicornis* (Family Megachilidae), with 6666 brood cells. The most abundant wasp species were the spider-predating digger wasp, *Trypoxylon figulus* (family Sphecidae), and the caterpillar-predating mason wasp, *Ancistrocerus nigricornis* (family Eumenidae), building 1659 and 931 brood cells, respectively. We found 36 taxa of higher trophic enemies of the orders Hymenoptera (clepto-parasites and parasitoids), Diptera (parasites), Coleoptera (predators) and Acari (parasites). Ten species attacked wasps, ten attacked bees, eight attacked both bees and wasps and eight attacked undetermined hosts. The most common enemy species were the gregarious chalcid wasp *Melittobia acasta*, which attacked 23 host species in 523 cells (Table S2) and the cleptoparasitic drosophilid *Cacoxenus indagator*, attacking three bee species in 1281 cells. The mean mortality due to natural enemies was 17.3% for wasps and 20.3% for bees. Full species lists can be found in Tables S1 and S2; and means for variables are given in Table S3.

TRAP NEST COMMUNITY STRUCTURE

Bee richness and total wasp and bee abundance were not related to plant species richness ($P > 0.1$), but there was a marginally significant relationship between the species richness of wasps and of plants (parameter value = 0.20, $P = 0.053$). Specifically, the species richness and abundance of spider-predating wasps were positively related to plant species richness (Table 1, Figure 2b and 3b). The abundances of spiders and spider-predating wasps were negatively correlated, while the abundances of spiders and herbivores were positively correlated. The abundance and species richness of the enemies were strongly positively related to the abundance and species richness of their hosts, respectively (Figure 4). Based on the AIC, mixed effect models without the plant composition as correlation structure almost always performed better than models including this term. Only the model for spider abundance in D-vac samples performed significantly better when plant composition was included as correlation structure. The coefficient λ was highest for the abundance of spiders and was generally larger for wasps than for bees (Table 1).

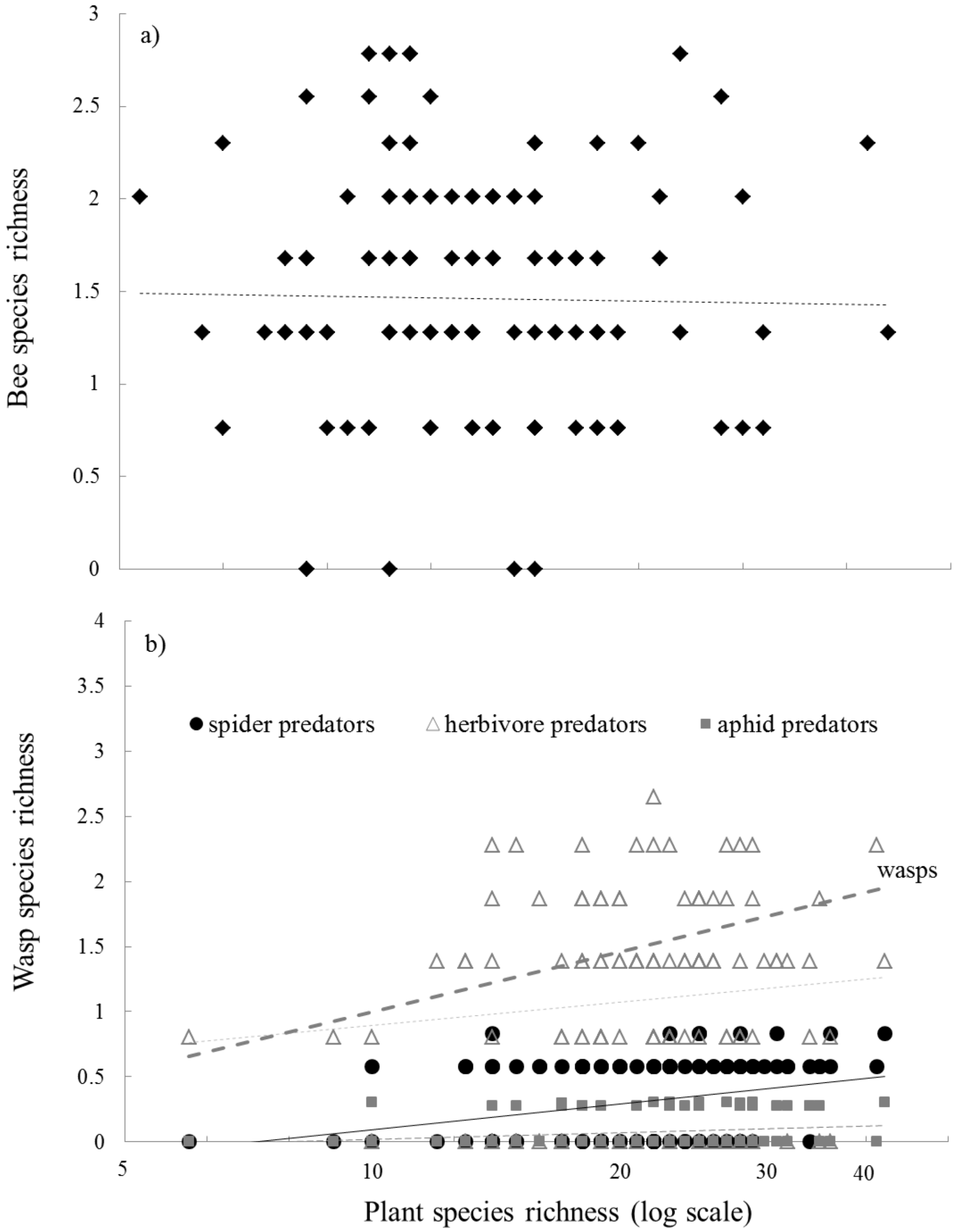

Figure 2. Relationship between plant species richness and species richness (all response variables were Box-Cox Power transformed; fit by linear regression lines) of a) bees and b) wasps: aphid-predating (squares and dashed line; all fit by linear regression lines), herbivore-predating (triangles and dotted line), and spider-predating wasps (circles and fine black line). Thick grey dashed line indicates the relationship for overall wasp species richness.

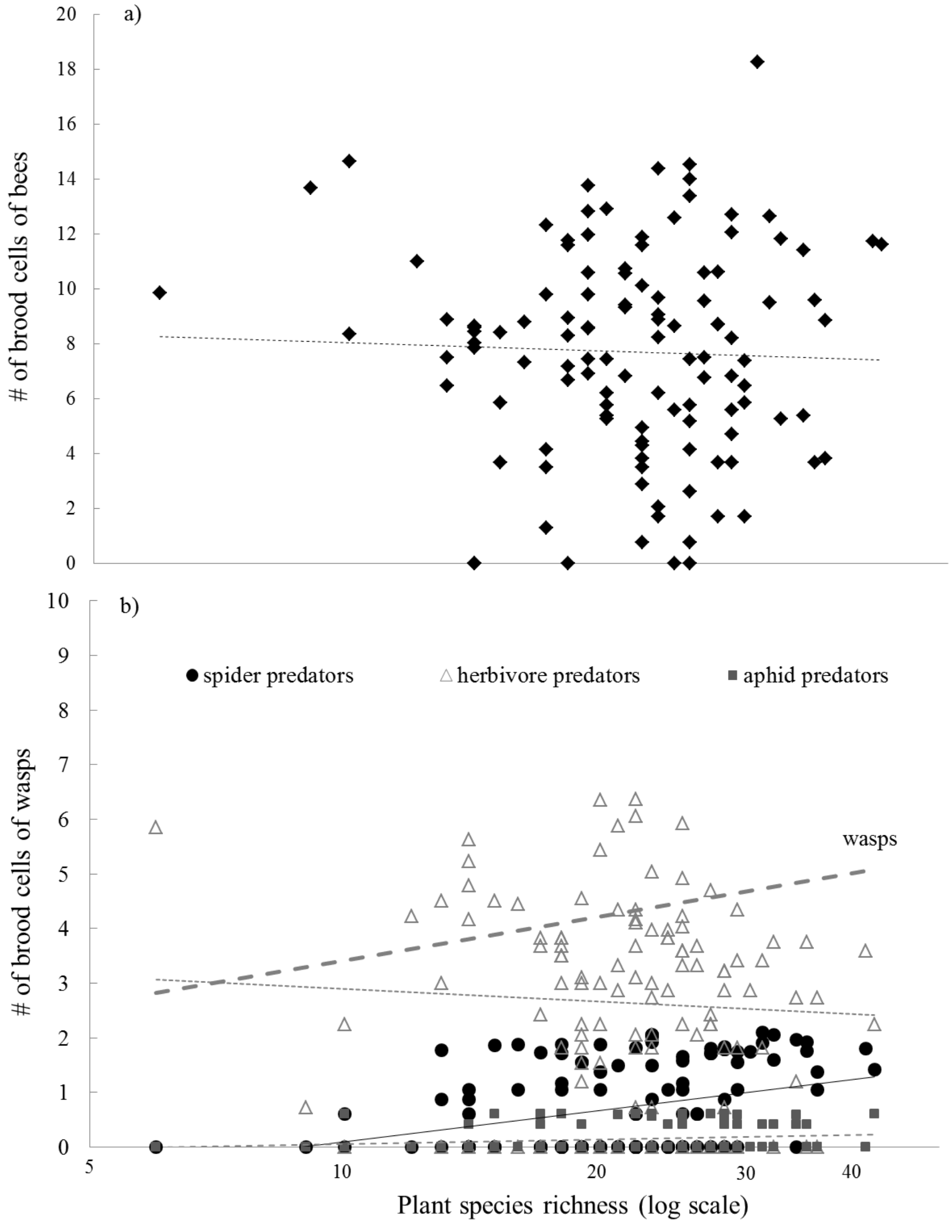

Figure 3. Relationship between plant species richness and number of brood cells (all response variables were Box-Cox Power transformed; fit by linear regression lines) of a) bees and b) wasps aphid-predating (squares and dashed line), herbivore-predating (triangles and dotted line), and spider-predating wasps (circles and fine black line). Thick grey dashed line indicates the relationship for overall wasp species richness.

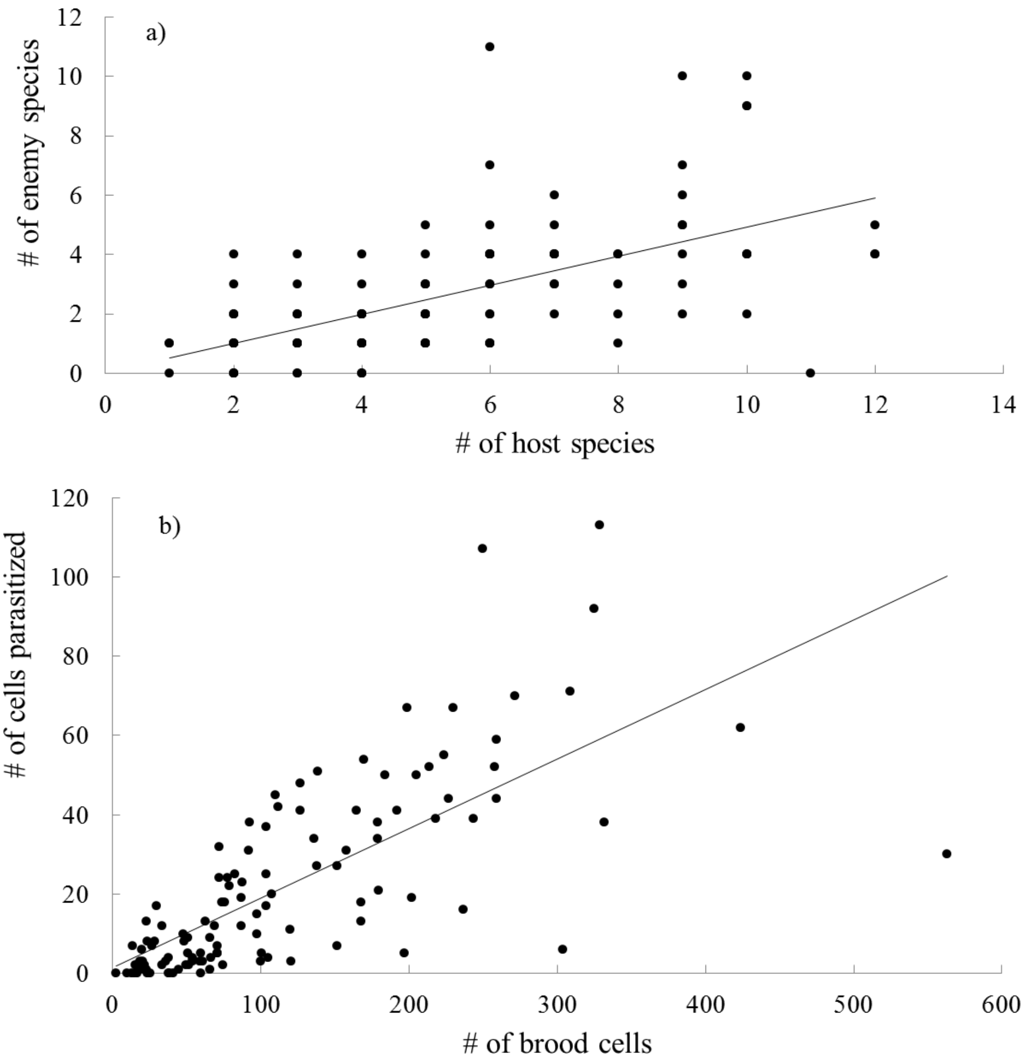

Figure 4. Relationship between a) enemy and host species richness and b) number of cells parasitized and number of brood cells, both fitted by linear regression lines.

FOOD-WEB STRUCTURE

The pooled quantitative food web is depicted in Figure 5. Neither quantitative nor qualitative food-web metrics were affected by plant species richness, but almost all were affected by the trap nest species richness (Table 2). Connectance was affected by vegetation height, but no other food-web metrics were affected by vegetation height or biomass. The AIC for all food-web metrics favors the model without the plant composition included.

Table 1. Parameter estimates from linear mixed effect models relating species richness and abundance of the trap-nest community and their prey to descriptors of vegetation and prey/predator abundance.

Response variables	*Explanatory variables* Plant species richness (log)	Vegetation height	Plant biomass	Additional variables in the model		Plant correlation coefficient	AIC with / without plant composition correlation
Species richness							
entire community	0.00 ns	0.03 ns	-0.05 ns	NA	NA	0.34	94 / 94
host species	0.08 ns	-0.07 ns	-0.08 ns	NA	NA	0.22	114 / 112
bees	-0.05 ns	0.08 ns	-0.03 ns	NA	NA	0.06	105 / 103
wasps	0.20 †	-0.14 ns	-0.09 ns	# arthropods	0.03 ns	0.49	117 / 117
aphid predators	0.15 ns	-0.16 ns	0.08 ns	# aphids	0.05 ns	<0.01	125 / 123
herbivore predators	0.06 ns	-0.01 ns	-0.17 ns	# herbivores	0.01 ns	0.26	127 / 125
spider predators	**0.27** *	-0.11 ns	0.11 ns	# spiders	-0.16 †	<0.01	112 / 110
enemies	-0.08 ns	-0.01 ns	0.01 ns	**host species richness**	**0.42 *****	0.15	58 / 56
Abundance (number of cells)							
# brood cells	-0.05 ns	-0.08 ns	-0.07 ns	NA	NA	<0.01	98 / 96
bees	-0.06 ns	-0.05 ns	-0.05 ns	NA	NA	<0.01	95 / 93
wasps	-0.06 ns	-0.11 ns	-0.09 ns	# arthropods	-0.08 ns	0.26	110 / 109
aphid predators	0.10 ns	-0.10 ns	0.06 ns	# aphids	0.03 ns	<0.01	127 / 125
herbivore predators	-0.05 ns	0.01 ns	-0.20 †	# herbivores	0.03 ns	0.28	81 / 79
spider predators	**0.20** *	-0.11 ns	-0.02 ns	**# spiders**	**-0.21***	<0.01	17 / 15
parasitized cells	-0.06 ns	-0.01 ns	0.02 ns	**# brood cells**	**0.54 *****	<0.01	118 / 119
Abundance of potential prey (D-vac)							
aphids	-0.01 ns	0.01 ns	0.16 ns	# aphid predators	0.08 ns	0.26	120 / 121
				# spiders	0.03 ns		
herbivores	0.14 ns	0.14 †	0.11 ns	# herbivore predators	-0.08 ns	0.14	76 / 74
				# spiders	**0.27 ****		
spiders	-0.07 ns	-0.05 ns	0.01 ns	# spider predators	-0.13 †	**0.56**	**67 / 76**
				# herbivores	**0.21 ***		

Additional variables measuring prey or predator abundance were added to the models as explained in the methods. Values of parameters come from REML models, with strips as random factors and the plant composition in the different subplots included as a correlation structure. Response variables were all Box-Cox power transformed, except species richness of aphid-predating wasps and abundance of spider-predating wasps, which were logarithmic transformed. *** P < 0.001, ** P < 0.01, * P < 0.05, † P < 0.1 and ns P > 0.1.

Table 2. Parameter estimates from linear mixed effect models relating food-web metrics to descriptors of vegetation and trap nest species

Response variables	*Explanatory variables*					
Food-web metrics	Plant species richness (log)	Vegetation height	Plant biomass	Trap nest species richness	plant correlation coefficient λ	AIC with / without plant composition correlation
quantitative						
vulnerability	-0.12 ns	0.03 ns	0.17 ns	**0.37 ***	0.15	28 / 26
generality	0.06 ns	0.13 ns	-0.20 ns	0.21 ns	0.08	48 / 46
interaction diversity	-0.11 ns	0.14 ns	-0.11 ns	**0.59 ****	0.07	37 / 34
qualitative						
vulnerability	-0.19 ns	-0.02 ns	0.27 †	**0.50 ****	<0.01	29 / 27
generality	0.11 ns	0.06 ns	-0.18 ns	**0.42 ***	<0.01	41 / 39
interaction diversity	0.01 ns	0.16 †	0.03 ns	**0.28 *****	<0.01	7 / 5
connectance	0.02 ns	**-0.31 ***	0.14 ns	**-0.68 *****	<0.01	29 / 27
nestedness	0.02 ns	0.01 ns	0.21 ns	**-0.57 *****	<0.01	33 / 31
# of compartments	0.11 ns	0.06 ns	-0.18 ns	**0.42 ***	<0.01	41 / 39

Values of parameters from REML models, with strips as random factors and the plant composition in the different subplots included as a correlation structure. *** P < 0.001, ** P < 0.01, * P < 0.05, † P < 0.1, and ns P > 0.1

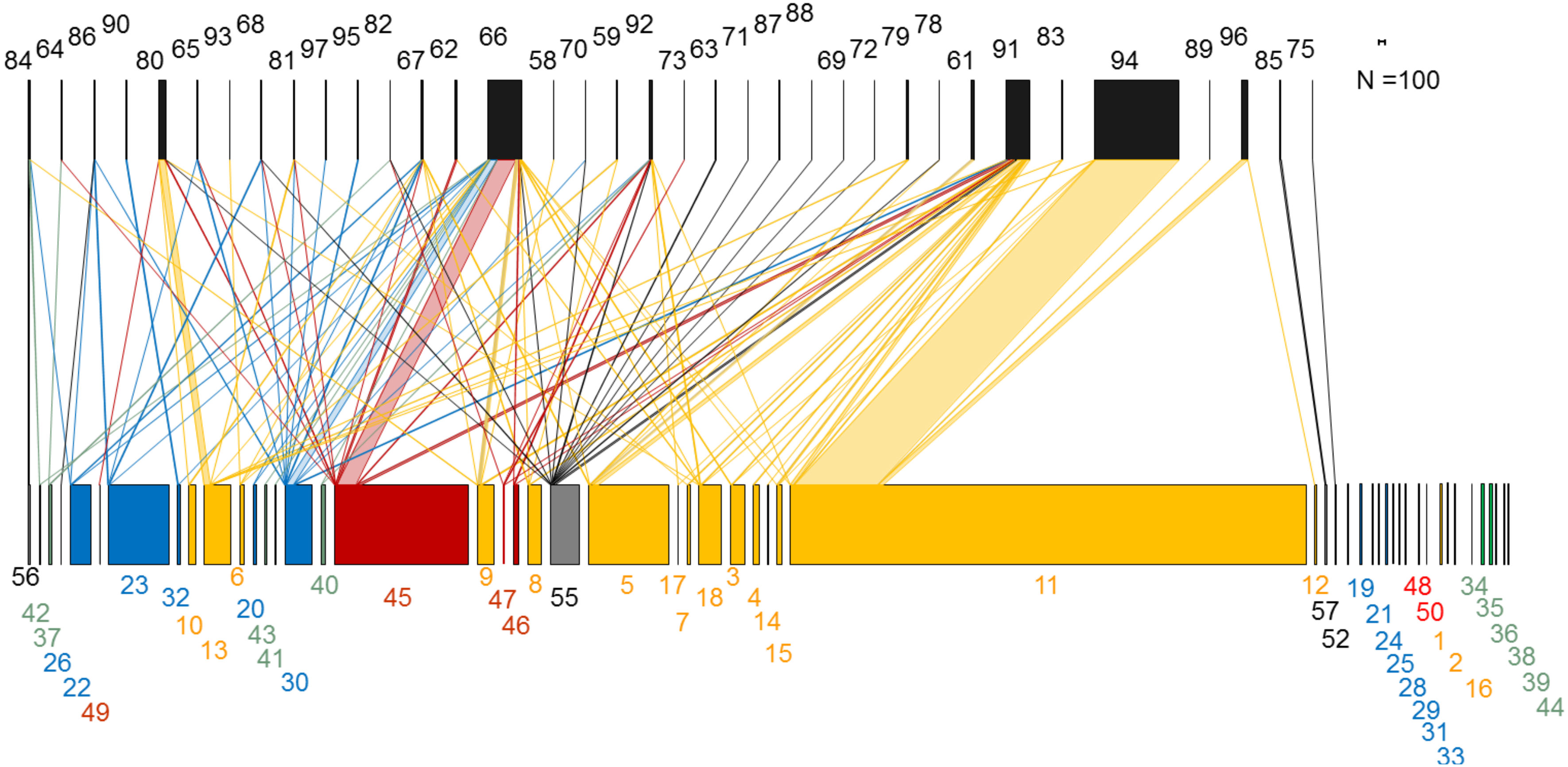

Figure 5. Quantitative host–enemy food webs from all diversity plots. Width of bars represents host and enemy abundance and width of links total number of interactions. Species richness: 34 hosts (lower bars) and 36 enemies (upper bars). Host functional groups: bees (yellow), aphid-predating wasps (green), herbivore-predating wasps (blue), spider-predating wasps (red) and undetermined groups (grey). Species codes are given in Table S1 & S2. Hosts and enemies are ordered to minimise the overlap of interactions

VEGETATION EFFECTS ON TRAP NEST COMMUNITIES

The multivariate analysis of the effect of the vegetation on the species composition of the entire trap nest community revealed marginally significant effects of plant species richness ($\chi^2 = 0.06$, $P = 0.07$; see Figure 6) and of vegetation composition ($\chi^2 = 2.43$, $P = 0.09$). Splitting the data into trophic guilds, we found that the community of bees was not affected by the vegetation measures or by the plant composition (all $P > 0.1$). In contrast, wasps were significantly affected by plant species richness ($\chi^2 = 0.18$, $P = 0.01$) and average vegetation height ($\chi^2 = 0.13$, $P = 0.03$). The latter effect was due to aphid-predating wasps ($\chi^2 = 0.35$, $P = 0.05$), and these wasps were also strongly influenced by the plant composition ($\chi^2 = 5.07$, $P = 0.01$, Figure 7).

Different wasp species seemed to be associated most strongly with certain plant species, for instance, members of the genus *Pemphredon* with *Stellaria media; Passaloecus vandelii* with *Cerastium sp.; Passaloecus gracilis* with *Cirsium arvense, Holcus lanatus* and *Convolvulus arvense*; most species of *Passaloecus* with *Pastinaca sativa*; *Psenulus pallipes* with *Equisetum arvense* and *Lolium perennis*; the latter two plant species were negatively associated with *Passaloecus* species.

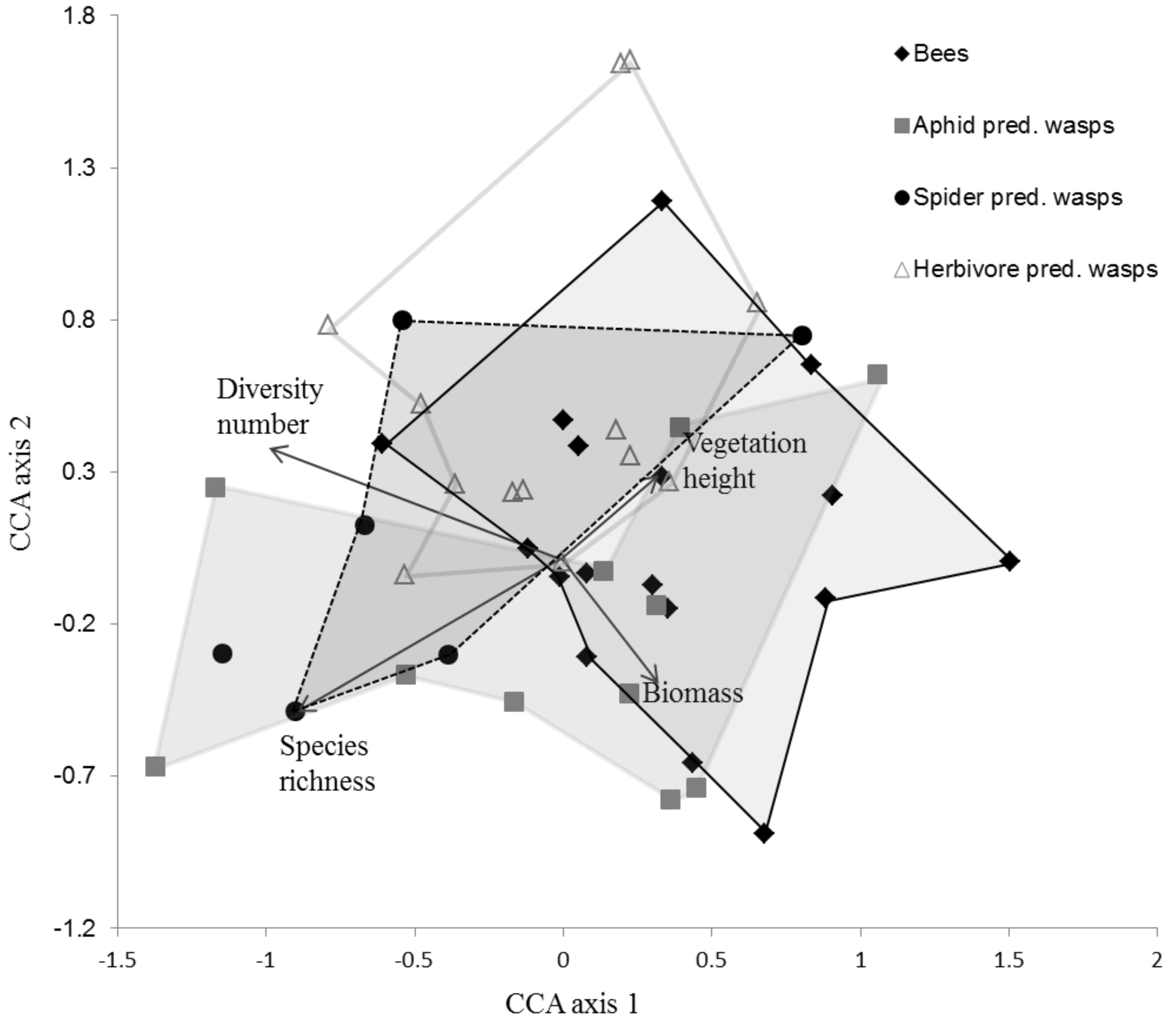

Figure 6. Canonical correspondence analysis for trap-nesting bee and wasp communities with vegetation measurements. Planes connect trophic guilds of: bees (diamonds), aphid-predating (squares), herbivore-predating (triangles) and spider-predating (circles) wasps.

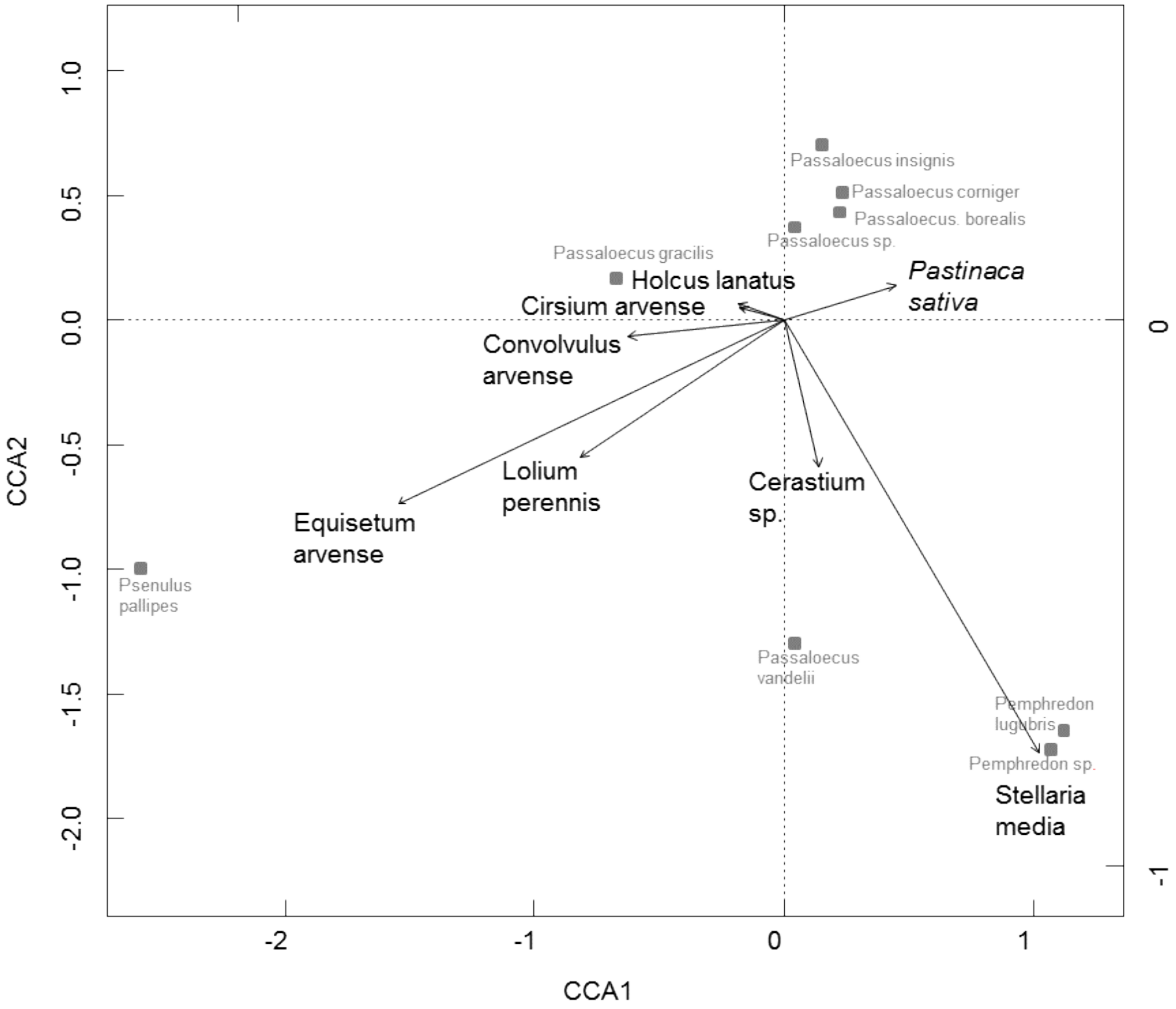

Figure 7. Canonical correspondence analysis for the aphid-predating wasp community (in grey) with the most influential plant species (in black). CCA axis 1 explains 25.5% ($\chi^2 = 0.66$, P = 0.005) and CCA axis 2 explains 19.9% ($\chi^2 = 0.57$, P = 0.005) of the variation.

DISCUSSION

The species richness and abundance of bees was not affected by plant species richness, but interestingly, the species richness of wasps and specifically the richness and abundance of spider-predating wasps were positively affected by plant species richness. Thus our results support the *resource heterogeneity* and *more individuals hypotheses* for wasps, but not for bees. Our prediction that the strength of the effect of plant diversity would decrease with increasing trophic level in the order 1) bees, 2) herbivore- and aphid-predating wasps and 3) spider-predating wasps, was not supported. However, in line with our hypothesis, the abundance and species richness of enemies was not related to plant diversity, but was strongly correlated with the abundance and species richness of their hosts (Albrecht *et al.* 2007; Ebeling *et al.* 2012). None of the qualitative or quantitative food-web metrics were related to plant species richness. Thus, contrary to our expectations, the effect of plant diversity on food-web structure was not stronger than on simple community richness. In the following, we discuss possible explanations of our results and some caveats of our study.

Changes in plant diversity mediate changes in open flower diversity, community biomass, and vegetation height, which in turn affect arthropod abundance and diversity (Hooper *et al.* 2005; Balvanera *et al.* 2006; Ebeling *et al.* 2012). In our study, the species richness of wasps and the richness and abundance of spider-predating wasps were positively affected by plant species richness. One explanation might be that solitary wasps can live as adults for several months (Buschini & Donatti 2012) and unlike their larvae, feed on pollen and nectar. High plant diversity results in a more abundant and stable supply of pollen and nectar resources for these species, resulting in higher wasp diversity. However, earlier studies of the effect of plant diversity on trap-nest diversity have found only small effects (Ebeling *et al.* 2012), or no effect on wasps (Albrecht *et al.* 2007).

The abundance of spider-predating wasps, dominated by the sphecid, *Trypoxylon figulus,* strongly increased with increasing plant species richness. An explanation might be that the species that are most strongly limited in their mobility by the weight of their prey might profit most from high plant diversity in the proximity of their nests. Generally, spider-predating wasps carry greater loads in relation to their body size than the other trap-nesting groups. Body size ratios of female wasps and the approximate size of their most abundant prey are the following: 1) for aphid-predating wasps, *Passaloecus borealis* (5.5-6.5 mm; De Beaumont 1964) with aphids (1-3 mm), ratio = 0.33; 2) for herbivore-predating wasps *A. nigricornis* (10-13 mm; Schmid-Egger 2004) with *Tortricidae* caterpillars (3-6 mm), ratio = 0.39; and 3) for spider-predating wasps *Trypoxylon figulus* (9-12 mm; De Beaumont 1964) with *Theridion impressum* (5-6 mm), ratio = 0.52. Thus, spider-predating wasps may be most strongly limited by the distances over which they must transport their prey, and hence seem to minimize this by selecting resource rich patches as breeding sites (Schoener 1971; Pyke, Pulliam & Charnov 1977).

We found no effect of plant species richness on the abundance of spiders, herbivores, or aphids. It is possible that, for spiders at least, we could not detect an effect because it was masked by top-down control, and hence stronger predation pressure by spider-predating wasps in plots with higher plant diversity. *Trypoxylon figulus* feeds mainly on spiders of the species *Theridion impressum, Mangora acalypha* and *Larinoides cornutus* (Araneidae and Theridiidae, Bruggisser 2010; Schüepp *et al.* 2011). The wasps can have a substantial negative effect on spider populations (Blackledge, Coddington & Gillespie 2003), because one female can catch 100-300 spiders in the course of a summer (Bristowe 1941). In our study every brood cell was filled with 5-15 spiders. Thus, with an average of ten spiders per larva, the 1732 brood cells would contain 17320 spiders caught by *Trypoxylon* wasps. Furthermore, the effect of spider-predating wasps in some strips was very great: five strips had on average only 0.8 spider-predating wasp cells per trap (0 to 28 brood cells per strip), but five others had an average of 27.2 brood cells per trap (102 to 583 cells per strip). In our system, strong population regulation of spiders by hymenoptera is seen in another member of the community, namely *Argiope bruennichi* by hornets (Bruggisser *et al.* 2012).

Moreover, the abundance of spiders and herbivores was strongly positively correlated, reflecting a bottom-up effect. Spiders are less mobile than flying insects and are strongly dependent on high prey abundances where they build their webs, as has been shown for *Argiope bruennichi* (Bruggisser *et al.* 2012).

The aim of the study was to explore if relationships between plants and higher trophic level communities were present at a small spatial scale. The results are intriguing since groups expected to react strongly - i.e., bees - showed no effect, while higher trophic levels - i.e., spider-predating wasps - did. This is an indication that the spatial scale of the diversity plots in our study was too small to detect effects on most trophic groups. Ebeling *et al.* (2012) also found no relationship between plant diversity and brood cell densities of bees. Their diversity plots were, similar to our experiment, within a short distance of each other. In contrast, they found an effect of flower richness, whereas abundance and diversity of bees in our experiment were not affected by flower diversity or abundance (Fabian Y. unpublished results). Albrecht *et al.* (2007) found a significant increase in bee abundance and species richness with increasing plant diversity. The distance between their sites with different plant diversities was on average 5 km and the average size of their sites was 1 ha; much larger than our plots. Thus, our small-scale experiment lies at the lower end of detectability of biodiversity effects for most groups, but interestingly functional groups showing a response are not the one most closely linked to plants (i.e., bees).

The complexity of biotic interactions should decrease even faster than simple species diversity and abundance (Tylianakis *et al.* 2008). Although the diversity and abundance of higher and lower trophic levels in the trap nests were strongly positively correlated, we detected no effect of plant diversity on the quantitative or qualitative food-web metrics. Surprisingly, connectance was negatively correlated with vegetation height, which might be due to a decreased accessibility of the trap nests for higher trophic levels when *Dipsacus fullonum,* the tallest species of our system, was abundant. In fact, the model with the logarithmically transformed cover of *Dipsacus fullonum* and trap-nest species richness showed a negative relationship between connectance and *D. fullonum* (parameter estimate = -0.29, P = 0.023). Thus, vegetation effects on food-web complexity were weaker than on simple species diversity and abundance, but their analyses revealed additional relationships. Again, the scale of our experiment might have been too small to detect effects of plant diversity on food-web structure.

In our mixed-effect model analyses, models with plant composition performed worse than models without, for all groups except spiders. Furthermore, the strongest effect of plant composition was found for spiders, and surprisingly one of the weakest was for bees. Earlier studies similarly found that the abundances of spiders were strongly affected by the plant community, acting through species composition (Schaffers *et al.* 2008), diversity (Bruggisser *et al.* 2012), or vegetation structure (Pearson 2009; Bruggisser *et al.* 2012). Spiders are less mobile than flying insects and where they build their webs is strongly dependent on high prey abundances and vegetation structure, which is closely linked to plant composition. Selective habitat choice, as has been suggested for *Argiope brunnichi* (Bruggisser *et al.* 2012), might explain this effect for spiders. Thus, including plant complexity in biodiversity models might be important for some groups and reveal unexpected results.

The present study has the advantage that all three vegetation variables are analyzed simultaneously. Earlier experimental studies treating the influence of plants mainly reported effects of species diversity without considering species composition (Knops *et al.* 1999; Haddad *et al.* 2009), although this has often been corrected for in recent studies (e.g. Koricheva *et al.* 2000; Schaffers *et al.* 2008). Plant community associations are likely to be a better predictor of arthropod species richness than plant species richness in a variety of ecosystems (Schaffers *et al.* 2008). Our ordination analysis revealed that vegetation height and composition structured the composition of aphid-predating wasps only. Their overall species richness and abundance did not depend on plant composition, as revealed in the mixed effect models, but individual wasp species were associated with particular plant species. The recognition of a relationship between arthropod and plant community composition and diversity can be highly valuable in conservation planning and land management. We thus, support the recommendations of earlier studies (Schaffers *et al.* 2008) that the species composition of plant communities deserves more attention in future work on arthropod assemblage, structure and diversity.

CONCLUSION

We conclude that small-scale plant diversity loss can affect cavity-nesting hymenoptera diversity and abundances. Specifically, analyzing different trophic groups can shed light on the underlying patterns governing these effects. Preserving even small biodiversity hotspots with a particular rich plant composition can benefit the conservation of biodiversity in agricultural landscapes.

ACKNOWLEDGEMENTS

We would like to thank Felix Amiet (Eumenidae, Sapygidae, Sphecidae), Hannes Baur (Parasitica) and Seraina Klopfstein (Ichneumonidae) for identification of uncertain specimens. Silvie Rotzetter and Valentine Renevey sorted the D-vac samples. We are grateful to Matthias Albrecht and Martin Schmidt-Entling for discussions and comments on trap-nest ecology. The experiment complies with current Swiss laws. This study was supported by the Swiss National Science Foundation (Grant 3100A0-113843 to LFB) and by the Fonds de recherche de l'Université de Fribourg, Switzerland. RPR was funded by the 214 FP7-REGPOT-2010-1 program (project 264125 EcoGenes).

APPENDIX

Table S1. Bee and wasp species in 117 trap nests, their number of occupied brood cells, and the number of cells attacked by their natural enemy species. Data from 10 experimental wildflower strips in the year 2008. Larval food: p / n = pollen and / or nectar, a = aphids; h = herbivores; s = spiders; na = not available. Species codes are used in Figure 5.

Code	Species	Food	# cells built	# cells attacked	Code	Species	Food	# cells built	# cells attacked
Apidae					**Sphecidae**				
1	*Hylaeus communis*	p/n	28	0	31	*Ectemius continuus*	h	1	0
2	*Hylaeus difformis*	p/n	7	0	32	*Isodontia mexicana*	h	31	6
3	*Hylaeus* sp.	p/n	212	13	33	*Nitela* sp.	h	5	0
4	*Chelostoma florisomne*	p/n	76	8	34	Sphecidae sp.	a	13	0
5	*Heriades truncorum*	p/n	1094	139	35	*Passaloecus borealis*	a	70	0
6	*Megachile centuncularis*	p/n	78	6	36	*Passaloecus gracilis*	a	61	0
7	*Megachile ericetorum*	p/n	44	10	37	*Passaloecus insignis*	a	43	5
8	*Megachile versicolor*	p/n	202	27	38	*Passaloecus corniger*	a	11	0
9	*Megachile* sp.	p/n	200	79	39	*Passaloecus vandeli*	a	3	0
10	*Osmia adunca*	p/n	100	2	40	*Passaloecus* sp.	a	70	6
11	*Osmia bicornis*	p/n	6666	1427	41	*Pemphredon lugubris*	a	20	1
12	*Osmia brevicornis*	p/n	21	4	42	*Pemphredon* sp.	a	16	5
13	*Osmia caerulescens*	p/n	332	118	43	*Psenulus pallipes*	a	22	2
14	*Osmia gallarum*	p/n	4	4	44	*Psenulus sp.*	a	2	0
15	*Osmia caerulescens/gallarum*	p/n	43	30	45	*Trypoxylon figulus*	s	1659	421
16	*Osmia cornuta*	p/n	2	0	46	*Trypoxylon* sp.	s	73	18
17	*Osmia* sp.	p/n	11	5	**Pompilidae**				
18	Apiformes sp.	p/n	322	42	47	*Agenioides cinctellus*	s	19	5
Eumenidae					48	*Auplopus carbonarius*	s	3	0
19	*Alastor atrops*	h	1	0	50	*Dipogon subintermedius*	s	5	0
20	*Allodynerus rossii*	h	55	5	49	*Dipogon* sp.	s	6	2
21	*Ancistrocerus antilope*	h	54	0	**Others**				
22	*Ancistrocerus gazella*	h	331	26	52	Symphyta sp.	na	6	4
23	*Ancistrocerus nigricornis*	h	931	21	55	undetermined host	na	392	62
24	*Ancistrocerus parietinus*	h	11	0	56	Host Braconidae 1	na	12	12
25	*Ancistrocerus* sp.	h	11	0	57	Host Braconidae 2	na	17	17
26	*Euodynerus notatus*	h	5	2					
27	*Gymnomerus laevipes*	h	18	0					
28	*Microdynerus timidus*	h	60	0					
29	*Symmorphus gracilis*	h	18	0					
30	Eumenidae sp.	h	298	160					
Total number of brood cells								13795	2695

Table S2. Enemies of bees and wasps in 117 trap nests and the number of brood cells attacked. Species codes are used in Figure 5. * Morphospecies.

Code	Species	# cells attacked
Hymenoptera		
Apidae		
59	*Coelioxys inermis*	4
58	*C. inermis/mandibularis*	3
61	*Stelis breviscula*	32
Chrysididae		
62	*Chrysis cyanea*	21
63	*C. ignita*	3
64	*Omalus auratus*	5
65	Chrysididae sp.	7
Eulophidae		
66	*Melittobia acasta*	523
Ichneumonidae		
67	*Ephialtes manifestator*	28
68-72	Ichneumonidae spp. 1-5*	16
73	Cryptinae sp.	1
75	Tryphoninae sp.	1
76	Campopleginae sp.	3
Gasteruptiidae		
78	*Gasteruption assectator*	2
Sapygidae		
79	*Sapyga decemguttata*	14
80	*S. quinquepunctata*	110
81	Sapygidae sp.	7
Chalcidoidea		
82	Pteromalidae sp.	1
Toryminae		
83	*Monodontomerus obsoletus*	14
Braconidae		
84-89	Braconidae sp. 1-6*	66
90	*Isodontia* parasites	3
Coleoptera		
91	*Trichodes alvearius*	376
92	*Megatoma undata*	69
Diptera		
93	*Anthrax anthrax*	12
94	*Cacoxenus indagator*	1281
95	Diptera larvae	2
Acari		
96	*Chaetodactylus osmiae*	90
undetermined		
97	species 1	1
Total		2695

Table S3. Arithmetic means ± standard errors, minimum and maximum values of the variables from trap nests, D-vac samples and vegetation measures of 117 subplots and 39 pooled food webs.

Variable	Mean ± SE	Min	Max
Species richness (Trap nest)			
entire community	9.5 ± 0.4	2	21
bee species	1.8 ± 0.1	0	6
wasp species	3.1 ± 0.2	0	10
aphid predators	0.5 ± 0.1	0	5
herbivore predators	1.5 ± 0.1	0	4
spider predators	0.6 ± 0.1	0	2
enemies	2.8 ± 0.2	0	10
Abundance (Trap nest)			
nr brood cells	118.0 ± 9.1	6	568
bee cells	80.7 ± 7.6	0	529
wasp cells	34.0 ± 3.7	0	238
aphid predator cells	2.7 ± 0.8	0	58
herbivore predator cells	15.6 ± 1.8	0	90
spider predator cells	15.1 ± 3.2	0	22
cells parasitized	23.0 ± 2.3	0	122
Quantitative food-web metrics			
vulnerability	1.5 ± 0.1	1.0	3.7
generality	1.5 ± 0.1	1.0	3.9
interaction diversity	2.0 ± 0.1	0.6	2.9
Qualitative food-web metrics			
vulnerability	1.8 ± 0.1	1.0	3.5
generality	2.0 ± 0.1	1.0	5.1
interaction diversity	2.0 ± 0.1	1.1	2.9
connectance	0.3 ± 0.0	0.2	0.5
nestedness	38.0 ± 1.9	20.9	63.1
# of compartments	2.8 ± 0.1	1	4
Prey abundance (D-vac)			
aphids (Aphidina)	52.6 ± 4.6	1	791
spiders (Araneae)	24.1 ± 4.1	5	130
herbivores	9.7 ± 0.6	0	33
beetles (Coleoptera larvae)	6.1 ± 0.7	0	27
butterflies (Lepidoptera larvae)	2.8 ± 0.2	0	16
barklice (Psocoptera)	1.0 ± 0.0	0	8
grasshoppers (Caelifera)	0.3 ± 0.0	0	3
Vegetation			
species richness	22.4 ± 0.6	6	42
biomass (g/m^2)	525.5 ± 14.4	247.8	1271.2
height (m)	1.4 ± 0.0	0.4	2.1

Chapter 4

The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem

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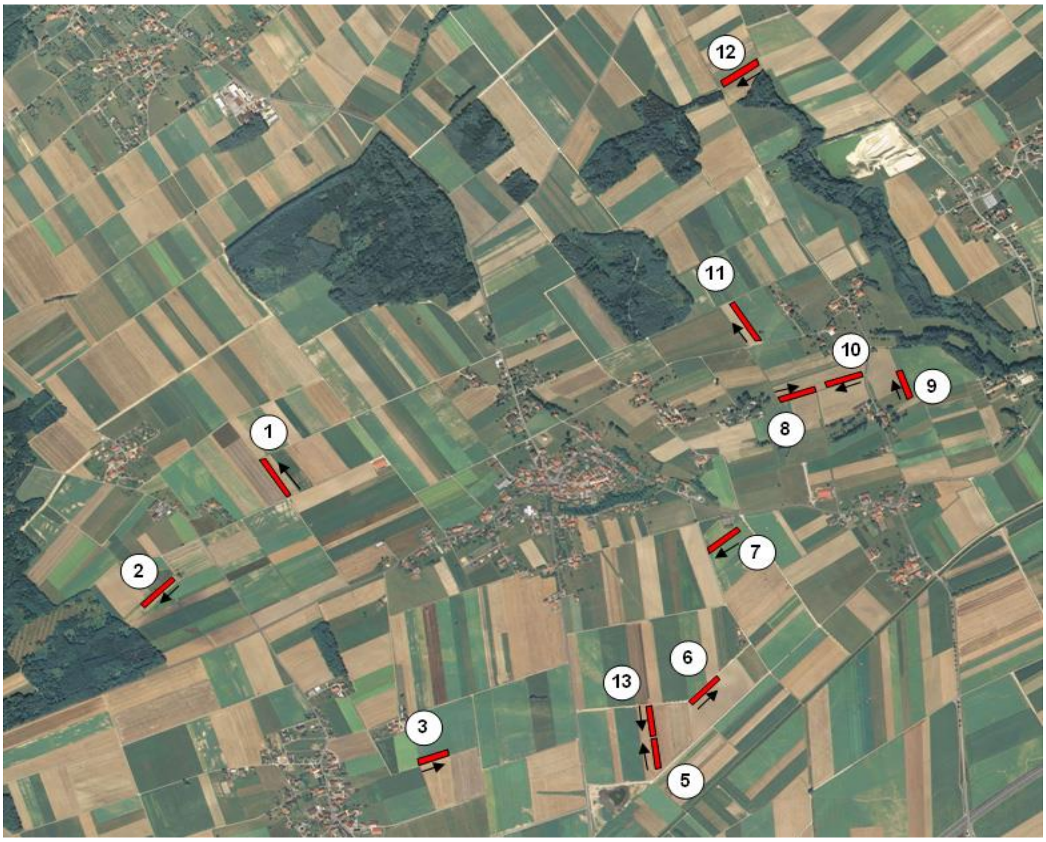
In revision in Journal of Animal Ecology



ABSTRACT

1. Understanding the environmental factors that structure biodiversity and food webs among communities is central to assess and mitigate the impact of landscape changes.

2. Wildflower strips are ecological compensation areas established in farmland to increase pollination services and biological control of crop pests, and to conserve insect diversity. They are arranged in networks in order to favour high species richness and abundance of the fauna.

3. We describe results from experimental wildflower strips in a fragmented agricultural landscape, comparing the importance of landscape, of spatial arrangement, and of vegetation on the diversity and abundance of trap-nesting bees, wasps and their enemies, and the structure of their food webs.

4. The proportion of forest cover close to the wildflower strips and the landscape heterogeneity stood out as the most influential landscape elements, resulting in a more complex trap nest community with higher abundance and richness of hosts, and with more links between species in the food webs and a higher diversity of interactions. We disentangled the underlying mechanisms for variation in these quantitative food-web metrics.

5. We conclude that in order to increase the diversity and abundance of pollinators and biological control agents and to favour a potentially stable community of cavity nesting hymenoptera in wildflower strips, more investment is needed in the conservation and establishment of forest habitats within agro-ecosystems, as a reservoir of beneficial insect populations.

Key-words: biological control agents, ecological compensation areas, ecosystem services, landscape ecology, parasitism, pollinators, quantitative food webs, trap nest, wildflower strip

INTRODUCTION

Intensification of agriculture in the 20th century has been accompanied by a drastic loss of biodiversity (Robinson & Sutherland 2002). Agricultural land use and conservation have traditionally been viewed as incompatible, but a cultivated landscape can be heterogeneous and provide many suitable habitats (Tscharntke *et al.* 2007). The identification of environmental factors that structure biodiversity among communities is central to the assessment of the impact of landscape changes (Jeanneret, Schupbach & Luka 2003) and the planning of conservation strategies. The proportion, quality and spatial arrangement of semi-natural habitats and overall habitat heterogeneity in the surroundings are thought to play major roles (Duelli 1997; Hendrickx *et al.* 2007; Fahrig *et al.* 2011; Gagic *et al.* 2011; Schüepp *et al.* 2011). Currently, however, there is limited knowledge of how these environmental factors also affect the functioning of entire food webs in agro-ecosystems (Albrecht *et al.* 2007).

The importance of conserving a high diversity of mutualistic and antagonistic interactions has been the subject of many studies (e.g. Thebault & Loreau 2006; Tylianakis, Tscharntke & Lewis 2007; Ings *et al.* 2009), especially because ecosystem services associated with species interactions such as pollination and biological control are of particular interest for human welfare (Balvanera *et al.* 2006; Cardinale *et al.* 2012). For example, the loss of interactions is predicted to threaten ecosystem stability and functioning, and like community composition, this also seems to be influenced by the spatial arrangement of habitat patches (Holt 1996) and landscape heterogeneity (Gagic *et al.* 2011). Locally, high compartmentalization in food webs is predicted to reduce the risk of species extinctions and increase food-web persistence (Stouffer & Bascompte 2011), and spatial effects are likely to influence this characteristic. However, although there is a solid body of research on how spatial structure is related to the stability of metacommunity food webs (McCann 2000; Pillai, Gonzalez & Loreau 2011), few generalizations exist about the consequences of spatial structure on food-web architecture. Rooney, McCann and Moore (2008) proposed general hypotheses about how food-web structure is related to spatial scale at the landscape level, but they do not easily apply to the arthropod-based systems studied here.

In Europe, agri-environmental schemes have been introduced to restore agricultural landscapes and enhance biodiversity. As a result, networks of ecological compensation areas have been created in farmland, including hedges, field margins and wildflower strips (Marshall & Moonen 2002). In Switzerland, wildflower strips are made up of a recommended plant mixture containing 24 herbaceous species sown inside fields or along their edges and are maintained for six years (Nentwig 2000). The species mixture was elaborated in order to benefit a maximal number of functional groups of animals, for ecosystem services (Haaland, Naisbit & Bersier 2011).

Different arthropod trophic groups respond differently to landscape changes (Jeanneret, Schupbach & Luka 2003; Klein, Steffan-Dewenter & Tscharntke 2004; Attwood *et al.* 2008), and the diversity of these groups can affect rates of ecosystem processes such as pollination (Garibaldi *et al.* 2011) and biological control (Thies *et al.* 2011), or the parasitism of beneficial parasitoids (Tylianakis, Tscharntke & Klein 2006). Trap-nesting bee and wasp communities are relevant indicators of ecological changes, due to their participation in all three types of interaction (Tscharntke, Gathmann & Steffan-Dewenter 1998). Like most species living in agro-ecosystems, they depend on complementary resources in different habitats (Klein, Steffan-Dewenter & Tscharntke 2004) for food (Ebeling *et al.* 2012) or nesting sites (Gathmann & Tscharntke 2002; Steffan-Dewenter & Leschke 2003; Sobek *et al.* 2009), and thus are sensitive to landscape heterogeneity (Fahrig *et al.* 2011) and the isolation of habitat patches (Holzschuh, Steffan-Dewenter & Tscharntke 2009; Krewenka *et al.* 2011; Schüepp *et al.* 2011).

In recent literature, trap-nest communities are usually split into three groups: bees, wasps, and higher trophic enemies (predators and parasitoids; Schüepp *et al.* 2011; Ebeling *et* *al.* 2012). However, while cavity-nesting wasps can act as biological control agents by collecting herbivorous arthropods (including phloem-sucking aphids (Aphididae), as well as larvae of smaller moths (microlepidoptera), leaf beetles (Chrysomelidae) and weevils (Curculionidae) (Tscharntke, Gathmann & Steffan-Dewenter 1998)), other wasp species feed on spiders (Araneae), which can themselves represent important biological control agents (Schmidt-Entling & Dobeli 2009). Thus, the wasps can usefully be separated into three trophic guilds, as predators of aphids, other herbivores, or spiders, to account for the ecological role of their prey.

Our trap-nest dataset derives from a temperate agro-ecosystem, reporting species richness, abundances and interaction frequencies between insect hosts and their enemies, and giving abundance estimations of the prey of trap-nesting wasps. We constructed food webs with quantitative trophic links and collected measures of local vegetation and landscape characteristics, to address the following questions:

1) What is the relative importance of vegetation characteristics, spatial arrangement and landscape composition to understand the structure of trap-nesting communities?
2) To which habitat characteristics (plant species richness, plant biomass, habitat isolation, landscape heterogeneity, and the cover of different landscape components) do bees, aphid-, other herbivore-, and spider-predating wasps, and their enemies respond?
3) To what extent is food-web structure (generality, vulnerability, link density, interaction diversity and compartment diversity) influenced by these habitat characteristics?

METHODS

FIELD MANIPULATIONS

This study was carried out as part of a larger project to assess the importance of biodiversity for the functioning of agricultural compensation zones, by manipulating the number of plant species and trophic levels in experimental wildflower strips (Bruggisser *et al.* 2012, Chapter

2). In spring 2007, twelve wildflower strips (hereafter strips) were sown in field margins around Grandcour, 10 km south of Lake Neuchatel in north-west Switzerland at an altitude of 479 m (coordinates: 46° 52' N 06° 56' E). The region (4 x 4 km) is characterized by a mosaic of arable fields (intensive agriculture), grasslands and forests, and the average distance between our strips was 1.6 ± 0.8 km. The strips each covered 864 m^2 and were either flat or slightly sloped. Within each strip, plant species diversity treatments (2, 6, 12 or 20 species) were repeated in four subplots in three blocks, with fencing treatments for other experiments as explained in (Chapter 2); a fourth block contained the complete 24 species wildflower mixture (Figure S1).

VEGETATION AND LANDSCAPE DESCRIPTORS

Vegetation characteristics. In the 14 subplots per strip (Fig. S1), the percentage cover of each plant species was determined in autumn 2008 using the Braun-Blanquet method (1964). The vegetation in each strip was characterised by the total plant species richness and by the average plant biomass (measured as leaf area index in each subplot) as a measure of productivity (see Chapter 2 for details).

Spatial arrangement of experimental wildflower strips. Strips were established to obtain a gradient of isolation from each other (min and max distances to the nearest strip were 118 m and 777 m, respectively; see Table S1). The spatial distribution of the strips (Figure S2) was characterised by the X and Y coordinates (in m) of the central point of each strip, relative to the centre of the study region. To capture more complex spatial structuring, we added the terms X^2, Y^2 and XY in the analyses (Borcard, Legendre & Drapeau 1992). Note that centring the coordinates removes the correlation between X and X^2, and between Y and Y^2 (Legendre & Legendre 1998).

Landscape composition, heterogeneity and habitat isolation. The landscape was categorised on the basis of official topographical maps (Bundes Amt Für Umwelt BAFU 2008; 1:5000) using Arcview GIS (version 3.3) and verified on field inspections in 2007 and 2008. For each strip, the surrounding landscape composition was characterised in a circle of radius 500 m (Gathmann & Tscharntke 2002). Correlations of landscape composition with trap-nest community richness and abundance were stronger at this radius than at smaller radii (100 m, 200 m, 300 m and 400 m; see supplementary methods), while larger radii would have resulted in too great an overlap between the surroundings of the different strips. Percentage cover was measured for six landscape elements: 1) agricultural fields, 2) extensive meadows (no fertilization, late mowing), gardens, orchards and hedges, 3) forest, 4) wildflower strips, 5) water bodies and 6) urban areas (roads and houses). Further details are given in Figure S2 and Table S1. The exponential of Shannon diversity (exp(H')) was calculated as a measure of landscape heterogeneity, with $H' = -\sum p_i \log(p_i)$, and p_i the proportion of each landscape category. Isolation was measured as the edge-to-edge shortest distance from a strip to the nearest wildflower strip (distance to wildflower strip in m). The distance from the strip to the nearest forest edge (distance to forest) was also measured, but due to its strong correlation with forest cover (Pearson's product-moment correlation, $r = -0.74$, df = 8, P = 0.014) and the correlations among landscape measures (Table S4), we used only forest cover in the surroundings (%) in the analyses. Forest stands were managed mixed forests of similar height (~25 m) dominated by spruce (*Picea abies*) and beech (*Fagus sylvatica*).

TRAP NESTS

Community composition. Trap nests enabled us to study species richness, abundance, and quantitative interactions of above-ground nesting hymenopterans and their natural enemies under standardized nesting conditions (Tscharntke, Gathmann & Steffan-Dewenter 1998). The nests consisted of 170-180 internodes of common reed *Phragmites australis* (length

20 cm), placed in plastic pipes (20 cm long, 10 cm diameter). The internal diameter of the reeds ranged from 2 to 8 mm. Each reed-filled plastic pipe was fixed on a wooden pole (1.5 m long) and protected by a 30 x 30 cm wooden roof (Figure S3). Fourteen trap nests were positioned in each strip (Figure S1) from mid-April until October 2008. After collection they were stored at 4°C for at least seven weeks to simulate winter. Some nests were destroyed while in place, including nearly all of those in two strips that were dismantled by a heron, thus in total 136 trap nests from 10 strips were analysed.

In spring 2009, all reed internodes containing brood cells were opened and counts made of the number of cells and the occurrence of (clepto-) parasites, parasitoids and predators (hereafter called "enemies") attacking the nest-makers (hereafter called "hosts"). Reeds were stored separately in glass tubes to collect emerging adult bees, wasps and their enemies for identification. If no adult emerged, features of the nest and larval food were used to identify the genus or (sub) family using the identification key of Gathmann and Tscharntke (1999). Empty brood cells of eumenid wasps were assumed to belong to the bivoltine *Ancistrocerus nigricornis*, since it was the only species for which offspring of the first generation emerged before trap collection (Krewenka *et al.* 2011). Species richness and abundance (number of brood cells) in each wildflower strip were recorded for the entire trap-nest community and separately for the following groups: pollen- and nectar-collecting bees (Apidae), aphid-predating wasps (Sphecidae of the genera *Passaloecus, Pemphredon,* and *Psenulus*), other herbivore-predating wasps (Eumenidae and Sphecidae, feeding on Chrysomelidae, Curculionidae, Caelifera, and microlepidoptera larvae), spider-predating wasps (Pompilidae and Sphecidae of the genus *Trypoxylon*), and enemies (see Tables S2 and S3). Note that the abundance of enemies was measured as the number of parasitized brood cells, and not the total number of emerging individual enemies.

Food-web metrics. Quantitative host-enemy interaction food webs were constructed for each strip and five food web metrics were calculated following Bersier *et al.* (2002; for formulae see Supplementary Methods) using the bipartite package (Dormann *et al.* 2009). *Vulnerability* is the weighted mean effective number of enemies per host species and *generality* is the weighted mean effective number of hosts per enemy species. *Link density* is the weighted mean effective number of links per species and *interaction diversity* is the Shannon diversity of interactions, which takes both the number and the evenness of interactions into account (Tylianakis, Tscharntke & Lewis 2007). *Compartment diversity* is a measure of the size homogeneity of compartments (subsets of a web that are not connected with other subsets). These metrics are often used as measures of food web complexity.

AVAILABILITY OF ARTHROPOD PREY

To estimate arthropod abundance, 14 vacuum samples were taken in each wildflower strip using a D-vac foliage hoover type SH 85C (Stihl, Dieburg, Germany). Measures were taken in May 2008, between 10:00 and 16:00 on dry and sunny days. This period covers both the peak in flight activity of early and abundant species (*Trypoxylon* and the bivoltine *Ancistrocerus nigricornis*), and the start of the peak of late species (*Ancistrocerus gazella* and *Passaloecus borealis*; Bellmann 1995). In the middle of each subplot the vegetation and ground in an area of 1 m^2 were vacuumed for two minutes. Collected arthropods were stored in ethanol and grouped into orders. The average aphid and spider abundances per strip were used as estimates of food availability for aphid- and spider-predating wasps, respectively (Table S1). Average abundances of Lepidoptera, Psocoptera, Coleoptera larvae and Caelifera were summed per strip and used as estimates of “herbivore” availability for other herbivore-predating wasps. In the analyses treating all wasps, the average abundances of all six prey groups were summed and included as “arthropods”.

STATISTICAL ANALYSES

All statistical analyses were conducted in R 2.12.1 (R Development Core Team 2012). The species richness and abundance (number of brood cells) of bees, wasps and enemies were log transformed to meet the assumptions of constant error variance and normality of errors (Sokal & Rohlf 1995). Explanatory variables were standardized to zero mean and unit variance using the function *scale*. Correlations among the vegetation and landscape variables were tested using a Pearson correlation matrix. Several of the landscape elements were strongly correlated with landscape heterogeneity (Table S4), so they were excluded from the analyses.

Variance partitioning of the trap nest community with respect to landscape and vegetation characteristics. In order to compare the explanatory power of the three sets of environmental descriptors (vegetation composition, landscape composition and spatial arrangement) for the trap nest community data, we used a variance partitioning method (Hofer, Bersier & Borcard 2000), using the function *varpart* in vegan (Oksanen *et al.* 2011). This application uses partial redundancy analysis (RDA) with the community matrix as dependent variable and the sets of environmental descriptors as independent variables (Blanchet, Legendre & Borcard 2008). The analysis was applied for the entire community and for seven subsets: all host species, bees, wasps, aphid-, other herbivore-, and spider-predating wasps, and all enemy species. To reduce the asymmetry of the heavily skewed abundance data, they were log-transformed according to Anderson, Ellingsen & McArdle (2006). The rationale of variance partitioning can be simply understood using the example of a single response variable in a linear framework: to measure the effect of one independent variable, one firstly regresses the data with all other variables (the variables to be excluded) and extracts the residuals, which are then regressed with the variable of interest. Adjusted R square values (R^2_{adj}) can be used to represent the percentage variance in the data explained by each independent variable (Peres-Neto *et al.* 2006); note that R^2_{adj} can be negative, which must be interpreted as an absence of explanatory power. In our case, the response variable was multidimensional (observations – i.e., strips – can be seen as points in an n-dimensional space whose axes are the abundances of the n species) and we consequently used ordination approaches. Ordinations define a new system of axes where the variability of the data is expressed on few informative dimensions. RDA is a method of so-called "constrained" ordination, where the new axes are linear combinations of explanatory variables – in essence, it is a multiple regression for multidimensional data.

We have 10 observations (strips), so first summarized each set of environmental descriptors as a single composite variable to avoid over-fitting. This yielded a single explanatory variable for each environmental set, and thus avoided giving greater weight to sets of variables with more descriptors. To achieve this, we again relied on ordinations, and extracted the coordinates of the strips on the first ordination axis. For the vegetation composition, we conducted a correspondence analysis (CA) on the log-transformed cover of the 30 most abundant plant species (the first axis explained 20% of the variation in cover), and used principal component analyses (PCA) for the six square-root transformed landscape composition parameters and for the five spatial arrangement parameters of the strips (the first axes explained 65% and 53% of the variation, respectively). PCA is the standard method of dimension reduction; CA is a method of choice for abundance data, which typically includes many zeros, because shared absence of species is considered non-informative. Extensive explanations of these multivariate methods can be found in Legendre and Legendre (1997).

The RDA provided estimates of the percentage of variance due exclusively and in common to the three groups of descriptors. To test significance of the exclusive fractions, we applied a test with 9999 permutations using the function *anova*. To further inspect the relationship between the trap nest communities and individual variables, we performed a canonical correspondence analysis (CCA) for each full set of environmental descriptors. CCA is a method of constrained ordination customarily applied to test the effects of environmental variables on abundance data of communities; we used the function *cca* in vegan. We further applied the function *ordistep* with stepwise backward elimination of the least significant variables, to identify the descriptors that best explained the variation in trap nest communities.

Habitat characteristics affecting species richness, abundances, and food web metrics.

The effects of local vegetation (species richness and biomass), of landscape (percentage of forest cover and landscape heterogeneity) and of spatial arrangement (distance to the nearest wildflower strip) were modelled on the response variables species richness and abundance, for the entire community and for each functional group separately. For the analyses of aphid-, of other herbivore-, of spider-predating, and of all wasps, one variable that represents prey availability was added to the model. It was obtained from the D-vac sampling data, and was composed of the abundance of aphids, of other herbivores, of spiders, and of all these three groups, respectively. For enemy richness and abundance, the host species richness and abundance, respectively, served as a sixth variable, again expressing prey availability. To account for the possible dependence of the functional groups on their prey, the prey availability was always retained in all models.

First, we compared the AICs of the full generalized least squares (gls) models for each response variable with and without spatial auto-correlation structure in the residuals, based on the coordinates of the centre of each strip. We used five different spatial correlation structures following Zuur *et al.* (2009, Chapter 7.2.). The AIC of the simplest gls model without spatial correlation was always lowest, indicating that spatial autocorrelation is weak in our data (results not shown). However, this procedure does not account for the statistical dependence of the strips for which the surrounding landscapes overlap (see Figure S2). Consequently, we analyzed the data using gls models with a correlation structure induced by the pairwise proportional overlap between the experimental strips. Proportional overlap c_{ij} between strips i and j is the ratio of the shared area divided by the total area covered by both 500 m landscape radii. Our model is given by $y = X\beta + \varepsilon$ with y the vector of the response variable, X the matrix of explanatory variables (the first column contains 1 for the intercept), β the vector of parameters, and ε the vector of residuals. In our case, we consider $\varepsilon \sim \mathrm{N}(0, \Sigma)$ with

$$\Sigma = \delta^2 \begin{pmatrix} 1 & \cdots & 0 \\ \vdots & \ddots & \vdots \\ 0 & \cdots & 1 \end{pmatrix} + \lambda\delta^2 \begin{pmatrix} 0 & \cdots & c_{ij} \\ \vdots & \ddots & \vdots \\ c_{ij} & \cdots & 0 \end{pmatrix}.$$

The parameter λ determines the strength of the correlation structure induced by the overlap in landscape and δ^2 denotes the variance. To estimate the p-value of λ, we performed log-likelihood ratio tests between models with and without the correlation structure. The code for the models is available upon request to the corresponding author.

To avoid over-fitting we chose among models with one and two explanatory variables only (when appropriate, prey availability was included as a third variable not subjected to selection). We ran the 16 possible models (the first contains the intercept only, or when appropriate, the intercept and prey availability), and chose the one with the lowest AIC, provided the difference in AIC was larger than 2 relative to the best model with fewer variables; otherwise, we chose that with fewer variables.

Assumptions of normality of residuals were tested with Q-Q plots and Shapiro-Wilk tests. With correlation structure, the residuals must be "decorrelated" (in other words, made identically and independently normally distributed) before checking for normality. This is achieved by the following transformation: $\tilde{r} = L^T r$, with r and $\tilde{r}$ the vector of residuals and of transformed residuals, respectively; L^T is the transpose of the lower triangular matrix, L, from Cholesky decomposition of Σ^{-1}, the inverse of the matrix Σ (L^T can be thought of as the square root of the matrix Σ^{-1}; see Houseman, Ryan & Coull 2004).

The same procedure and explanatory variables (vegetation, landscape and spatial arrangement) were used to analyse the quantitative food web metrics: vulnerability, generality, link density, interaction diversity and compartment diversity. To account for the possible dependence of these metrics on species richness (Banasek-Richter *et al.* 2009; Dormann *et al.* 2009), the latter was always included in the models.

RESULTS

In total, 136 trap nests were collected with 17,243 brood cells of 38 hymenopteran host species (Table S2), which used 17.2% of all provided reeds. Thirteen species of bees were identified in 11,980 cells, with *Osmia bicornis* L. (Megachilidae, code 11 in Table S2) the most abundant. Twenty-five species of wasps were identified in 4,716 brood cells, including mason wasps (Eumenidae), digger wasps (Sphecidae) and spider wasps (Pompilidae). Records were dominated by the spider-predating *Trypoxylon figulus* L. (code 45) and the caterpillar-predating *Ancistrocerus nigricornis* Curtis (code 23). Enemies from 40 taxa (not all identified to the species level) were recorded, in the orders Hymenoptera (clepto-parasites and parasitoids), Diptera (parasites), Coleoptera (predators) and Acari (parasites). Nine taxa were specialized on wasps, ten on bees, seven attacked both bees and wasps, and 14 attacked undetermined species (Table S3). Mortality due to enemies, i.e., the number of parasitized cells divided by the total number of cells, was 19.7% for bee and 17.1% for wasp hosts. The most abundant generalist was *Mellitobia acasta* Walk. (Chalcidoidea: Eulophidae, code 66 in Table S3), a gregarious pupal parasitoid found attacking 596 brood cells of 23 species.

VARIANCE PARTITIONING OF THE TRAP NEST COMMUNITY

The three sets of descriptors together explained 17% and 15% of the total variation in the community composition of hosts and enemies, respectively. The variance partitioning revealed that landscape composition was the most important descriptor for the trap-nesting hosts and for their enemies, explaining exclusively 17% and 11% of the variation, respectively (Table 1).

Neither the spatial arrangement of the wildflower strips nor the plant composition explained a significant fraction of the variation in hosts and enemies. After applying backward elimination of the landscape composition variables, the CCA analyses (Figure S4) identified forest cover as the most significant element for hosts (*F* = 1.8, P = 0.003) and for enemies (*F* = 2.0, P = 0.005).

Table 1. Partitioning of the variation in community composition explained by plant composition, wildflower strip spatial arrangement, and landscape composition. Uppercase: A, B, C is the variance explained by each set, including the shared variance. Lowercase: a, b, c is the variance explained exclusively by each set. The adjusted R^2 values are given. ** P< 0.01, * P< 0.05, † P< 0.1.

			Total variance (including shared variances) explained by			Variance explained exclusively due to		
Response variable	Total variation (SS)	Un-explained variation %	Plants A	Landscape B	Spatial arrangement C	Plants a	Landscape b	Spatial arrangement c
All species	1841	83	0.03	0.13	0.02	0.00	0.15 *	-0.01
all hosts	1314	83	0.01	0.14	0.00	0.01	0.17 **	0.00
bee hosts	632	83	-0.04	0.16	-0.04	0.04	0.20 *	0.02
wasp hosts	682	82	0.06	0.12	0.04	-0.02	0.13*	-0.02
-aphid predators	238	75	0.11	0.13	0.08	0.01	0.15 †	-0.01
-other herbivore predators	536	79	0.08	0.12	0.05	0.00	0.16 *	-0.01
-spider predators	123	91	0.00	0.13	0.02	-0.08	0.08	-0.05
enemies	513	85	0.06	0.09	0.05	-0.01	0.11 †	-0.03

TRAP NEST COMMUNITY STRUCTURE

Landscape variables were by far the most important in explaining community richness and abundance (Table 2). Forest cover had a positive effect on the species richness of hosts in general, on wasp and aphid-predating wasp richness, and on the total abundance of brood cells. Landscape heterogeneity had a positive effect on total species richness in the trap nests, on the species richness of bees and of aphid-predating wasps, and a negative effect on the abundance of other herbivore-predating wasps. An effect of spatial arrangement was detected only for the abundance of wasps, which was negatively affected by the distance to the closest wildflower strip. Vegetation variables were significant only in three instances: plant richness had a positive effect on host richness, whereas plant biomass negatively affected the species richness of other herbivore-predating wasps and the abundance of spider-predating wasps. Prey availability had a significant effect in most cases on the richness of the various functional groups, but not on their abundance, with the exception of the enemies, whose abundance was positively correlated with host abundance. Including the correlation structure to account for the statistical dependence of strips always yielded significantly better models, with the exception of the species richness of spider-predating wasps (for which $P = 0.056$).

Table 2. Parameter estimates and their significance from the best fitting generalized linear models relating species richness and abundance of the trap-nest community to descriptors of vegetation, landscape and spatial arrangement, and of prey availability for higher trophic levels.

			Vegetation				Landscape				Spatial		
	Prey availability		Species richness		Biomass		Forest cover		Heterogeneity		Distance to wildflower strip		λ
	β	p	*β*	p	*β*	p	*β*	p	*β*	p	*β*	p	p-value
Species richness													
total community	NA	NA	-	-	-	-	-	-	**0.17**	**0.002**	-	-	**0.032**
all hosts	NA	NA	**0.08**	**<0.001**	-	-	**0.15**	**0.005**	-	-	-	-	**<0.001**
bees	NA	NA	-	-	-	-	-	-	**0.25**	**<0.001**	-	-	**<0.001**
wasps	**0.13**	**0.042**	-	-	-	-	**0.21**	**0.005**	-	-	-	-	**<0.001**
aphid predators	**0.32**	**0.001**	-	-	-	-	**0.20**	**0.020**	**0.22**	**0.002**	-	-	**<0.001**
other herbivore predators	**0.32**	**0.011**	-	-	**-0.27**	**0.025**	-	-	-	-	-	-	**0.035**
spider predators	0.03	0.378	-	-	-	-	-	-	-	-	-	-	0.056
enemies	**0.09**	**0.008**	-	-	-	-	-	-	-	-	-	-	**<0.001**
Abundance													
number of brood cells	NA	NA	-	-	-	-	**0.18**	**0.005**	-	-	-	-	**<0.001**
bee cells	NA	NA	-	-	-	-	-	-	0.45	0.120	-	-	**<0.001**
wasp cells	0.04	0.364	-	-	-	-	-	-	-	-	**-0.38**	**0.011**	**<0.001**
aphid predators	0.02	0.382	-	-	-	-	0.41	0.16	-	-	-	-	**0.032**
other herbivore predators	0.18	0.089	-	-	-	-	-	-	**-0.43**	**<0.001**	-	-	**<0.001**
spider predators	-0.12	0.340	-	-	**-0.12**	**0.001**	-	-	-	-	-	-	**<0.001**
enemies	**0.61**	**<0.001**	-	-	-	-	-	-	-	-	-	-	**0.010**

The prey availability for the analyses of wasps and their subgroups is the abundance of their corresponding prey groups; prey availability for species richness of enemies is the number of host species; prey availability for abundance of enemies is the number of brood cells. A dash indicates parameters that were not included in the set of best-fitting models and thus were not estimated. Prey availability variables were always included in the models, except those indicated by NA (not applicable).

FOOD-WEB STRUCTURE

Landscape variables were again by far the most important in explaining the quantitative food web metrics. The proportion of forest in the surroundings positively affected vulnerability, generality, link density, and interaction diversity (Table 3). Landscape heterogeneity had a negative effect on vulnerability and a positive effect on interaction diversity. An effect of spatial arrangement was detected for generality and link density, both negatively affected by the distance to the closest wildflower strip. Vegetation variables were significant only for compartment diversity, which was positively affected by plant species richness and biomass.

The importance of forest cover for the food-web structure can be seen when comparing the pooled quantitative food web for the five strips with lowest forest cover in the surroundings (0 to 1.6%) with that for the five with highest forest cover (6.2 to 17%) (Figure 1). A higher diversity of hosts and enemies and higher link density are the hallmarks of food webs with greater forest cover in the surroundings.

It is interesting to further explore the results of Table 3 in terms of the effects on the proportions of generalist vs. specialist species, and the changes in the shapes of distributions of interaction frequencies. For each of the five dependent variables, we discuss only the explanatory variable with the strongest effect. Increasing vulnerability and generality with forest cover might occur through three non-exclusive mechanisms: 1) a decreased proportion of “specialists” (i.e., hosts that only ever have one enemy species, or enemies that have only one host) in sites with greater forest cover nearby; 2) a greater diversity of interactions by the “generalists” in such sites (i.e., more enemies for each “generalist” host and more hosts for each “generalist” enemy); 3) a more equitable distribution of enemies or of hosts, which can be measured by interaction evenness. For vulnerability we found that all three mechanisms play a role: in strips with greater forest cover in the surroundings 1) there tended to be fewer “specialist” hosts (r = -0.63, df = 8, P = 0.053; Figure S5a), 2) “generalist” host species were usually attacked by more enemies (14 out of 17 species had a positive relationship between the effective number of enemies and forest cover; binomial test P = 0.013; Figure S5b) and 3) the interaction evenness of hosts increased with greater forest cover (*r* = 0.75, df = 8, P = 0.012; Figure S6). In contrast, for generality, forest cover in the surroundings did not affect the proportion of specialists (*r* = 0.03, df = 8, P = 0.93; Figure S7a), and there was no overall trend for the number of hosts per “generalist” enemy to increase with forest cover (7 out of 16 species had positive relationships; binomial test P = 0.80; Figure S7b). However, the enemies with the greatest numbers of hosts did show an increase in the number of hosts with increasing forest cover (positive values on the y axis in Figure S7b), and the interaction evenness of enemies increased with greater forest cover (*r* = 0.79; df = 8, P = 0.007; Figure S6), leading to the overall positive effect of forest cover on generality.

The link density can be expressed as the arithmetic mean of vulnerability and generality, so we do not discuss further the effect of forest cover on this variable. We note, however, the negative relationship between link density and community species richness (i.e., the "size" of the food webs), which contrasts with a strong positive relationship for the qualitative link density (slope = 0.52, P = 0.002, not shown). This indicates that species-rich systems have very uneven distributions in interaction frequency at the species level compared to species-poor systems (Banasek-Richter *et al.* 2009). Interaction diversity considers frequency distributions globally for the food-web matrix (and not for each species individually as does link density). The significant positive relationship with forest cover is due to a greater number of trophic interactions in strips with high forest cover (*r* = 0.65, df = 8, P = 0.042), and not to a change in evenness of the interactions at the food-web level (*r* = 0.17, df = 8, P = 0.63; Figure S8). The positive effect of plant species richness on compartment diversity might simply be a consequence of an increased proportion of enemy species with only one host (*r* = 0.65, df = 8, P = 0.039; Figure S9) and hosts with only one enemy species (*r* = 0.68, df = 8, P = 0.030), making it more likely that the web is split into compartments.

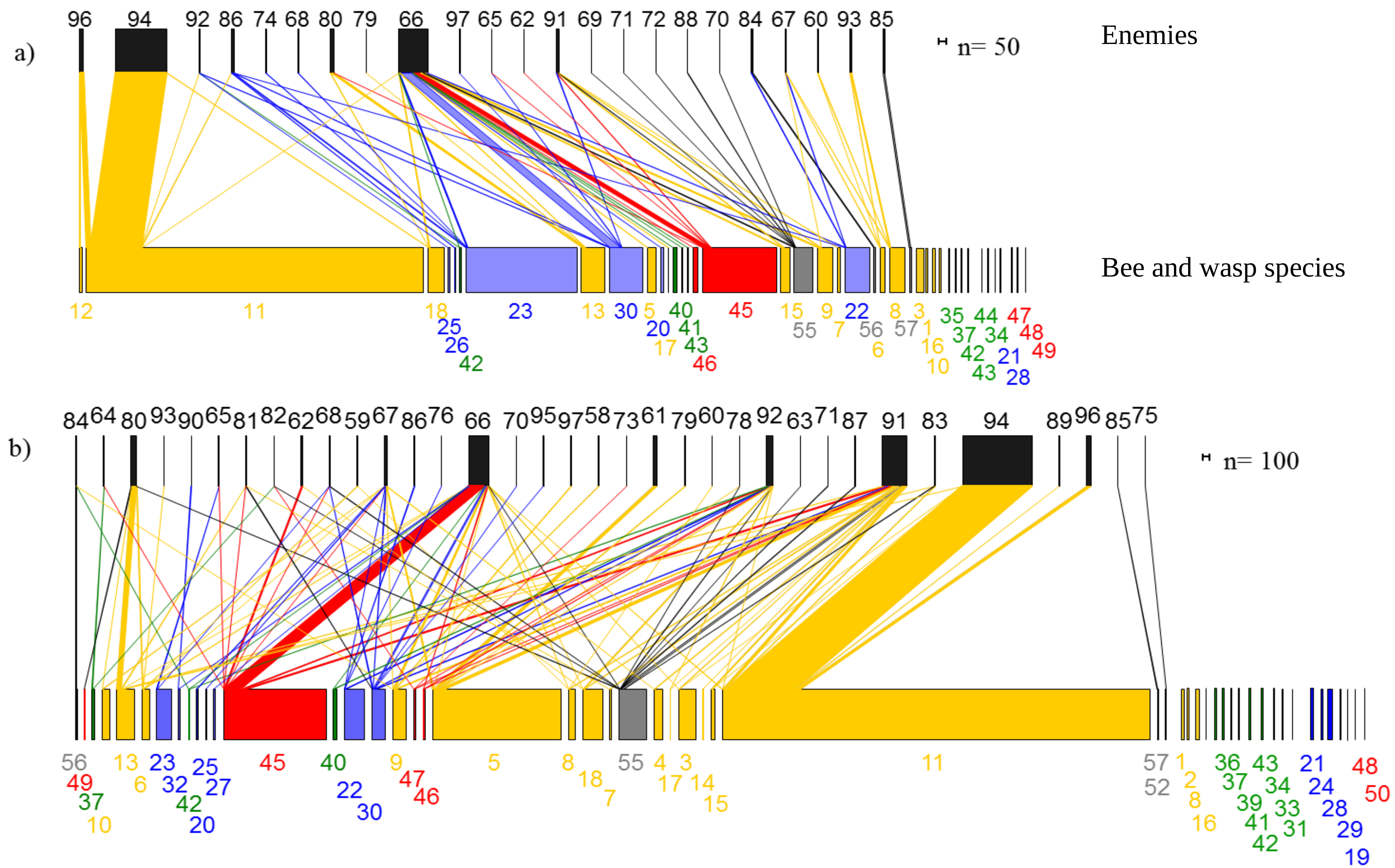


Figure 1. Quantitative host–enemy food webs from five wildflower strips with a) low forest cover (0 to 1.6%; total number of trap nests = 66) and b) high forest cover (6.2 to 17%; total number of trap nests = 70) in a 500 m radius. Note that the scale of the upper panel is double that of the lower. Width of bars represents host and enemy abundance, and width of links number of interactions. Species richness: a) 41 hosts and 23 enemies; b) 53 hosts and 34 enemies. Host functional groups: bees (yellow), aphid-predating wasps (green), other herbivore-predating wasps (blue), spider-predating wasps (red) and undetermined groups (grey). Upper bars represent enemy abundance (black). Species codes are given in Tables S2 and S3. Hosts and enemies are ordered to minimise the overlap of interactions.

Table 3. Parameter estimates and their significance from the best fitting generalized linear models relating food web metrics to descriptors of community species richness, vegetation, landscape and spatial arrangement.

			Vegetation				Landscape				Spatial		
	Community species richness		Species richness		Biomass		Forest cover		heterogeneity		Distance to wildflower strip		
Food web metric	β	p	β	p	β	p	β	p	β	p	β	p	λ p-value
vulnerability	0.23	0.056	-	-	-	-	**0.50**	**<0.001**	**-0.41**	**0.001**	-	-	**<0.001**
generality	**-0.58**	**0.001**	-	-	-	-	**0.92**	**<0.001**	-	-	**-0.34**	**0.009**	**<0.001**
link density	**-0.38**	**<0.001**	-	-	-	-	**0.71**	**<0.001**	-	-	**-0.20**	**0.011**	**<0.001**
interaction diversity	-0.11	0.220	-	-	-	-	**0.09**	**<0.001**	**0.08**	**0.032**	-	-	**<0.001**
compartment diversity	**-1.10**	**0.004**	**1.70**	**0.001**	**1.06**	**0.006**	-	-	-	-	-	-	**<0.001**

Community species richness was included in all models. A dash indicates parameters that were not included in the set of best-fitting models and thus were not estimated.

DISCUSSION

In our system, landscape composition played a greater role than either vegetation characteristics within the strips or spatial arrangement in determining the composition of the trap-nest community. Furthermore, species richness and abundances were most strongly affected by the landscape composition (forest cover and landscape heterogeneity) in the surroundings, followed by the vegetation (plant species richness and biomass) and the spatial arrangement of the wildflower strips (distance to the nearest wildflower strip). Our results also show that the foremost influence on community functioning, as measured by the quantitative food-web structure, was the landscape in the surroundings, followed by the spatial arrangement and the vegetation in the strips. Interestingly, the strongest effect on most quantitative food-web measures (vulnerability, generality, link density and interaction diversity) was due to the forest cover in the surroundings, and this effect was apparent even after accounting for the effects on species richness.

The affiliation of cavity-nesting wasps to forest and woody habitat in agricultural landscapes has been demonstrated in other systems (Holzschuh *et al.*, 2009; Schüepp *et al.* 2011). Forests are thought to provide dead-wood nesting sites with cavities made by wood-boring insects, which are otherwise not present in primarily cleared or simple habitats (Sobek *et al.* 2009). Hence, forests house source populations of wild bees and wasps, which spill over into adjacent agricultural habitats, potentially enhancing pollination and biocontrol (Tscharntke *et al.*, 2005). We found that the presence of woody habitats not only enhanced community diversity, but also strongly affected food-web complexity.

The differences in food-web structure mediated by forest cover were not merely a consequence of differences in community composition, but also in behaviour. Mechanisms behind the positive effect of forest cover on quantitative vulnerability and generality included: 1) the presence of fewer hosts with a single enemy species, 2) a greater diversity of interactions by generalist hosts, 3) a greater effective number of hosts for the highly generalist enemies, and 4) a higher interaction evenness of both hosts and enemies. The mechanism driving the positive effect of forest cover on quantitative interaction diversity was due to a higher number of interactions. To our knowledge, this is the first study to disentangle the underlying causes of variation in the quantitative food-web measurements.

In theory, highly diverse communities with higher connectance (link density/species richness) are more stable (Gravel *et al.* 2011), thus our study underlines the importance of forest cover for the diversity of natural pollinators and biological control agents and for the maintenance of intact and stable food webs in agro-ecosystems.

Similarly, when comparing the importance of vegetation characteristics, landscape composition and the spatial arrangement of wildflower strips for the composition of the trap-nest community, we found that the landscape components surrounding the strips were by far the most important descriptors. A large fraction of the variation remained unexplained, which may result from the setting of our study: strips can be considered as islands of favourable habitat in a hostile matrix of agricultural land, and the establishment of particular species may be strongly affected by stochastic events. Our variance partitioning analyses showed that forest cover was the only variable showing significant effects within this high level of variability. Thus, we think that wildflower strips should not be viewed as a network of patches of a single habitat type with their inhabitants behaving as a self-supporting meta-community (Leibold *et al.* 2004), but rather as elements of a heterogeneous landscape that bridge agricultural and late succession habitats.

The tree species richness, canopy height and age of forests are important parameters determining the species richness and abundance of cavity-nesting communities (Sobek *et al.* 2009). In our study, these parameters were very similar for all strips, but for a better understanding of the importance of forest patches for ecosystem services in agricultural land, future studies should consider these characteristics. Furthermore, identification of the pollen collected by solitary bees and the origin of prey collected by wasps might provide further insights into the importance of wildflower and forest patches in agro-ecosystems.

Availability of resources may increase if the landscape matrix surrounding a focal patch includes other suitable habitat types. In our system, high landscape heterogeneity promoted the species richness of trap-nest communities in general and specifically the richness of bees and aphid-predating wasps. However, landscape heterogeneity was strongly correlated with the cover of several habitat types, and in particular was negatively correlated with the cover of agricultural fields (r = -0.98, P < 0.001), so it is possible that some taxa are responding to the presence of particular habitats, rather than to heterogeneity itself. For instance, in contrast to all other taxa, we found that herbivore-predating mason wasps (Eumenidae) were less abundant when the surroundings were more heterogeneous, a result in line with the findings of Steffan-Dewenter (2003). These wasps may forage mainly in agricultural fields and thus be limited by the cover of cultivated habitat. They were abundant in our wildflower strips, and studies on their role in biological control, including the foraging distances that they cover, would be promising avenues for future research. Our study highlights the importance of distinguishing between different wasp trophic guilds for the evaluation of the contribution of agricultural compensation zones to bio-control. Furthermore, the species richness of these guilds was strongly affected by the abundance of their prey, which underlines the importance of including prey availability in statistical models.

Radmacher and Strohm (2010) found that *Osmia bicornis*, the most abundant species in our study, maximizes its foraging rate by temporally and locally specialized foraging behaviour within the agricultural landscape. In early season they mainly visited oak (*Quercus* sp.) and maple (*Acer* sp.) trees, whereas in late season they used poppy (*Papaver* sp.) and buttercup (*Ranunculus* sp.) with only traces from other plant families. This use of multiple food sources and habitats might underlie the positive correlation between bee diversity and landscape heterogeneity in our study.

Holt (1996) predicted strong effects of habitat isolation and spatial structure on food web topology. We found negative effects of isolation (distance to the next strip) not only on the abundance of wasps, but also on the generality and link density of the food webs. By accounting for the spatial overlap in the surrounding landscape between the experimental wildflower strips we always achieved a better fit of the models compared to the simple model lacking spatial autocorrelation, and this was in contrast to the results with classical spatial autocorrelation approaches (Zuur *et al.* 2009). We thus present a new method to incorporate a correlation matrix into linear models for applied use in future landscape ecology research.

The abundance and diversity of trap-nesting bees and wasps was high in our study (mean of 126.8 brood cells per standardized trap nest), compared to research in forest patches (Sobek *et al.* 2009; 27.4 brood cells), grasslands (Albrecht *et al.* 2007; Schüepp *et al.* 2011; Ebeling *et al.* 2012; with 170.5, 70.5 and 90.3 brood cells, respectively) and agricultural areas (Holzschuh, Steffan-Dewenter & Tscharntke 2010; 61.3 brood cells). Thus, managed wildflower strips appear to provide favourable habitat with access to food resources for pollinators and biological control agents. The species richness of plants in the wildflower strips positively affected the total species richness of the trap-nesting community and the compartment diversity of their food webs. Theory suggests that higher levels of compartment diversity should increase the stability of food webs (McCann 2000; Stouffer & Bascompte 2011), which emphasizes the need to promote plant diversity within agricultural landscapes. However, in contrast to other studies reporting a positive relation between bee species richness and plant species richness (Albrecht *et al.* 2007 with 9-18 naturally occurring plant species; Ebeling *et al.* 2012 with 1-16 sown species), we did not detect an effect of vegetation on bees. This may be because plant species richness only limits the richness of pollinators when it is very low, whereas it was relatively high (30-50 species) in all strips in our study.

In line with other studies, the diversity and abundance of the highest trophic level, the enemies, were strongly positively affected by the species richness and abundance of hosts, but not by vegetation and landscape characteristics (Steffan-Dewenter 2003; Albrecht *et al.* 2007).

Caveats of our study

We could only sample ten wildflower strips and thus small sample size surely limits the statistical power of our analyses, but, in our opinion, this is counterbalanced by the high sampling effort for each strip (on average 1700 individuals collected per strip). Consequently, most effects were strong and consistent across analyses.

Another caveat is that some hosts and enemies could not be determined to species level, which may have biased some of the food-web metrics. We tried to minimise this, by identifying these individuals as far as possible, by delimiting morphospecies, and by using information on nest and food remains to assign them to a trophic group. The proportion of individuals not determined to the species level was 11.1%, within the range of other studies (e.g. Albrecht *et al.* 2007 and Schüepp *et al.* 2011, with 2.8% and 27.4% respectively); typically, these were individuals that did not complete development, or were heavily damaged by their enemies.

CONCLUSION

Wildflower strips are intended to provide pollinators and biological control agents with sufficient pollen and herbivore prey to maintain high abundances and species richness close to agricultural fields. We found that communities in the strips strongly respond to the presence of forest habitats, with effects on species richness, abundance, and food-web complexity. In order to ensure long-term sustainability of wild bee and wasp communities and consequently their ecosystem services as pollinators and biological control agents, we conclude that it is not only necessary to maintain and restore a dense network of flower-rich habitat patches in agricultural landscapes, but also to conserve a diverse landscape mosaic that includes forest areas.

ACKNOWLEDGEMENTS

We would like to thank Felix Amiet, Seraina Klopfstein and Hannes Baur for identification of some specimens, Martin Entling for providing reference specimens, David Frey and Till Sander for help in the field, laboratory and with Arcview, Sven Bacher for discussions on statistics and ecology, and Jacques Studer`s Eco-office for important help in the planning of this experiment. We are very grateful to three anonymous reviewers for their constructive suggestions, which greatly improved the manuscript. The study was supported by the Swiss National Science Foundation (grant 31003A-113843 to LFB).

AUTHOR CONTRIBUTIONS

PK, LFB, YF and OB designed and AA, OB, NS and YF established the experiment; YF and RPR performed the analysis and YF wrote the first draft; REN, YF, PK and LFB revised the manuscript.

APPENDIX

SUPPLEMENTARY METHODS

Mantel tests

We performed simple Mantel tests to determine the area over which landscape composition best explained the abundance of bees, wasps and enemies. We used Bray-Curtis dissimilarities for the percentage cover of the seven landscape categories at a distance of 100, 200, 300, 400 and 500 m and the abundance of the trap-nest community members, and performed 10,000 permutations (Goslee & Urban 2007).

In accordance with Gathmann and Tscharntke (2002), measurements at a radius of 500 m best explained species abundances in the trap nests (r = 0.37, P = 0.02).

Food web metrics

Quantitative, weighted measures of link density, generality, vulnerability, interaction diversity and compartment diversity based on Shannon's entropy were calculated following Bersier *et al.* (2002), Tylianakis *et al.* (2007) and Dormann *et al.* (2008). Quantitative metrics are weighted to incorporate the total inflow and outflow (based on frequency of interactions) of individuals per species. Diversity of hosts ($H_{N,k}$) and diversity of consumers ($H_{P,k}$), were calculated for each species k as:

$$H_{\mathrm{N},k} = -\sum_{i=1}^{s} \frac{b_{ik}}{b_{\bullet k}} \log_2 \frac{b_{ik}}{b_{\bullet k}} \qquad H_{\mathrm{P},k} = -\sum_{j=1}^{s} \frac{b_{kj}}{b_{k\bullet}} \log_2 \frac{b_{kj}}{b_{k\bullet}}$$

The sum of column $b_{\bullet k}$ is the number of individuals attacked by taxon k and the sum of row $b_{k\bullet}$ is the number of individuals attacking taxon k. The frequency of interactions from taxon i to taxon k, and from taxon k to taxon j, is represented as b_{ik} and b_{kj}, respectively.

The "reciprocals" of the diversities ($n_{N,k}$ - effective number of hosts and $n_{P,k}$ - effective number of consumers) give the theoretical number of species interacting in equal proportion that would yield the same value of *H*:

$$n_{\mathrm{N},k} = \begin{cases} 2^{H_{\mathrm{N},k}} \\ 0 \qquad \text{if } b_{\bullet k} = 0 \end{cases} \qquad n_{\mathrm{P},k} = \begin{cases} 2^{H_{\mathrm{P},k}} \\ 0 \qquad \text{if } b_{k\bullet} = 0. \end{cases}$$

Generality (G_q), the weighted average effective number of host species per consumer, and **vulnerability** (V_q), the weighted average effective number of consumer species per host, were calculated as:

$$G_q = \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{\mathrm{N},k} \qquad V_q = \sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{\mathrm{P},k}$$

where $b_{\bullet\bullet}$ is the total number of attacked individuals.

Link density (LD_q) is the number of links per species, calculated as the arithmetic mean of generality and vulnerability:

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} 2^{H_{\mathrm{P},k}} + \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} 2^{H_{\mathrm{N},k}}\right).$$

Interaction Diversity (ID_q) was calculated as:

$$ID_q = -\sum_{i=1}^{s}\sum_{i=1}^{s} p_{ij} \ln(p_{ij})$$

where p_{ij} is the number of cells of host *i* attacked by enemy *j*, divided by the grand sum of the number of attacked cells. It uses Shannon's diversity index with links rather than individuals as the basis of measurement.

Compartment diversity (CD_q) was calculated as:

$$CD_p = \exp\left(-\sum_{i=1}^{n} p_i \ln(p_i)\right)$$

where p_i is the fraction of all species in the ith of n compartments. The number of compartments in a web is defined as the number of sub webs with no link to any other sub web (Tylianakis, Tscharntke & Lewis 2007).

SUPPLEMENTARY TABLES

Table S1. Means ± standard errors, minimum and maximum values of each variable across the 10 strips.

	Mean ± SE	Min	Max
Species richness			
total community	40.8 ± 3.1	29	54
all hosts	26.6 ± 1.7	19	35
bees	9.9 ± 0.9	5	15
wasps	14.7 ± 1.4	9	22
aphid predators	4.3 ± 0.7	2	8
other herbivore predators	6.5 ± 0.7	4	10
spider predators	3.1 ± 0.3	2	4
enemies	12.7 ± 1.3	8	19
Abundance (number of cells)			
average number of brood cells per trap	124.7 ± 16.8	29.1	193.3
bee cells	86.2 ± 13.9	7.5	144.1
wasp cells	34.8 ± 6.4	16.0	70.1
aphid predators	2.5 ± 0.7	0.2	7.4
other herbivore predators	18.0 ± 4.3	6.0	54.6
spider predators	13.9 ± 5.3	0.9	44.2
cells parasitized	23.1 ± 17.4	4.3	58.4
Food web metrics			
vulnerability	1.7 ± 0.2	1.2	3.2
generality	2.3 ± 0.2	1.2	3.9
link density	2.0 ± 0.2	1.2	2.9
interaction diversity	2.1 ± 0.2	1.5	2.8
compartment diversity	2.6 ± 0.5	1.0	6.3
Average abundance in D-vac samples			
arthropods	103.1 ± 10.1	63.7	175.0
aphids	48.3 ± 7.5	28.7	103.6
other herbivores	10.1 ± 1.5	3.1	16.2
spiders	42.4 ± 6.6	15.3	86.9
Vegetation measurements			
Plant species richness	39.6 ± 2.1	30	50
Plant biomass (g/m^2)	522.9 ± 28.6	379.6	686.2
Landscape cover (%)			
Agricultural fields	75.0 ± 3.1	58.4	90.5
Forest	6.3 ± 2.1	0.0	17.0
Orchards, hedges, extensive meadows	9.7 ± 2.1	2.8	19.6
Wildflower strips	0.6 ± 0.2	0.0	1.7
Water bodies	0.2 ± 0.1	0.0	1.3
Roads and houses	8.0 ± 1.2	3.6	16.3
Landscape heterogeneity	2.4 ± 0.2	1.5	3.6
Distance to closest wildflower strip (m)	291.0 ± 72.2	118	777
Distance to closest forest (m)	291.4 ± 87.4	20	861

Table S2. Trap-nesting host Hymenoptera in the 10 experimental wildflower strips. Species codes are used in Figure 1. Larval food: p/n = pollen and nectar; a = aphids; h = other herbivores; s = spiders. The species groups used in the analyses are defined as follows: "bees" = Apidae; "wasps" = Eumenidae, Sphecidae, Pompilidae; the three subgroups for wasps (aphid-, other herbivore- and spider-predating wasps) are defined according to their larval food.

Nesting species	# brood cells	Larval food	Code	Nesting species	# brood cells	Larval food	Code
Apidae				**Sphecidae**			
Hylaeus communis	58	p/n	1	*Ectemius continuus*	1	h	31
H. difformis	7	p/n	2	*Isodontia mexicana*	31	h	32
Hylaeus sp.	301	p/n	3	*Nitela* sp.	5	h	33
Chelostoma florisomne	124	p/n	4	Sphecidae sp.	27	h	34
Heriades truncorum	1819	p/n	5	*Passaloecus borealis*	73	a	35
Megachile centuncularis	138	p/n	6	*P. gracilis*	62	a	36
M. ericetorum	53	p/n	7	*P. insignis*	43	a	37
M. versicolor	219	p/n	8	*P. corniger*	11	a	38
Megachile sp.	250	p/n	9	*P. vandeli*	3	a	39
Osmia adunca	119	p/n	10	*Passaloecus* sp.	83	a	40
O. bicornis	7980	p/n	11	*Pemphredon lugubris*	20	a	41
O. brevicornis	21	p/n	12	*Pemphredon* sp.	20	a	42
O. caerulescens	362	p/n	13	*Psenulus pallipes*	22	a	43
O. gallarum	4	p/n	14	*Psenulus* sp.	2	a	44
O. caerulescens/gallarum	87	p/n	15	*Trypoxylon figulus*	1823	s	45
O. cornuta	12	p/n	16	*Trypoxylon* sp.	73	s	46
Osmia sp.	13	p/n	17	**Pompilidae**			
Apidae sp.	413	p/n	18	*Agenioides cinctellus*	27	s	47
Eumenidae				*Auplopus carbonarius*	9	s	48
Alastor atrops	1	h	19	*Dipogon subintermedius*	5	s	50
Allodynerus rossii	55	h	20	*Dipogon* sp.	6	s	49
Ancistrocerus antillope	61	h	21	**Others**			
A. gazella	498	h	22	Symphyta sp.	6	-	52
A. nigricornis	1253	h	23	undetermined hosts	512	-	55
A. parietinus	11	h	24	Host Braconidae 1	12	-	56
Ancistrocerus sp.	16	h	25	Host Braconidae 2	17	-	57
Euodynerus notatus	5	h	26				
Gymnomerus laevipes	34	h	27				
Microdynerus timidus	74	h	28				
Symmorphus gracilis	18	h	29				
Eumenidae sp.	344	h	30				
Total number of brood cells					17 243		

Table S3. Higher trophic level ("enemy") species in the 10 experimental wildflower strips. Species codes are used in Figure 1. Host group: B = bees; W = wasps; G = bees and wasps; O = enemies of undetermined hosts. *Morphospecies.

Enemy species	# Cells attacked	Host group	Code
Hymenoptera			
Apidae			
Coelioxys inermis	4	B	59
C. mandibularis	4	B	60
C. inermis/mandibularis	3	B	58
Stelis breviscula	61	B	61
Chrysididae			
Chrysis cyanea	22	G	62
C. ignita	3	O	63
Omalus auratus	5	W	64
Chrysididae sp.	7	W	65
Eulophidae			
Mellitobia acasta	596	G	66
Ichneumonidae			
Ephialtes manifestator	45	G	67
Ichneumonidae spp. 1-5*	17	O	68-72
Cryptinae sp.	1	W	73
Lissonota sp.	2	W	74
Tryphoninae sp.	1	O	75
Campopleginae sp.	1	W	76
Ophion sp.	5	O	77
Gasteruptiidae			
Gasteruption assectator	2	B	78
Sapygidae			
Sapyga decemguttata	16	B	79
S. quinquepunctata	127	G	80
Sapygidae sp.	7	G	81
Pteromalidae			
Pteromalidae sp.	3	W	82
Toryminae			
Monodontomerus obsoletus	15	B	83
Braconidae			
Braconidae spp. 1-6*	77	O	84-89
Isodontia parasites	3	W	90
Coleoptera			
Trichodes alvearius	407	G	91
Megatoma undata	108	G	92
Diptera			
Anthrax anthrax	13	B	93
Cacoxenus indagator	1544	B	94
Diptera larvae	2	W	95
Acari			
Chaetodactylus osmiae	106	B	96
undetermined			
Species 1	1	W	97
Total	3208		

Table S4. Correlations among variables. Cell entries are Pearson’s correlation coefficient, n=10. ***P<0.001, **P<0.01, *P<0.05, †P<0.1

		Cover (%)						landscape hetero-geneity	Distance (m) to next		Vegetation	
		forest	extensive meadows	gardens, hedges & orchards	wildflower strips	roads & houses	water bodies		wildflower strip	forest	species richness	bio-mass
Cover (%)	agricultural fields	-0.61 †	-0.80 **	-0.78 *	-0.07	-0.12	0.29	-0.98 ***	0.20	0.81 **	-0.23	-0.07
	forest		0.12	0.12	0.11	-0.43	0.14	0.56	-0.19	-0.74 *	0.02	-0.25
	extensive meadows			0.92 ***	0.08	0.16	-0.25	0.86 ***	-0.26	-0.51	0.18	0.29
	gardens, hedges & orchards				0.28	0.07	-0.40	0.86 ***	-0.52	-0.46	0.02	0.42
	wildflower strips					-0.44	-0.39	0.17	-0.72 *	0.22	-0.67 *	0.40
	roads & houses						-0.47	0.01	0.65 †	0.06	0.51	-0.06
	water bodies							-0.27	0.12	-0.10	-0.12	-0.36
	landscape heterogeneity								-0.33	-0.75 *	0.17	0.11
Distance (m) to next	wildflower strip									0.03	0.60 †	-0.57
	forest										-0.17	0.04
Vege-tation	species richness											-0.57

SUPPLEMENTARY FIGURES

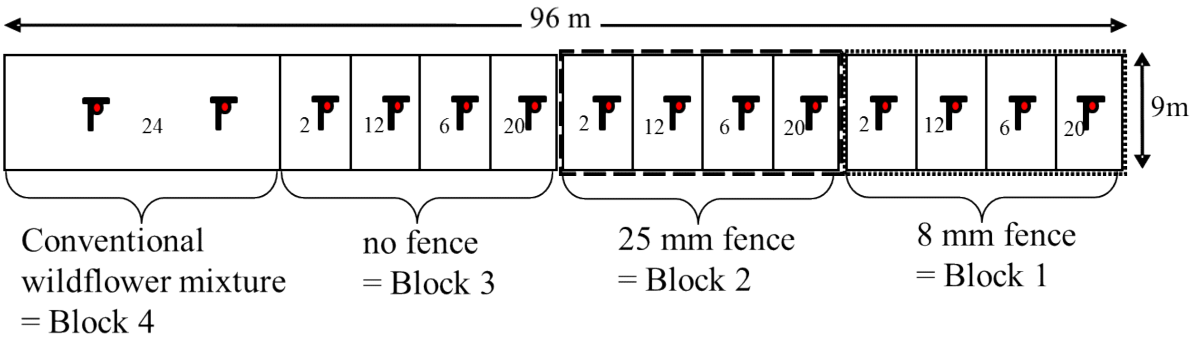


Figure S1. Arrangement of the 14 trap-nests (red circles) within subplots in the experimental wildflower strips. Numbers indicate sown plant species richness. Strips were divided into four blocks of equal size: 1. fence with 8 mm mesh (dotted-line), 2. fence with 25 mm mesh (dashed-line), 3. no fence, and 4. conventional wildflower mixture without fence. Note that fencing had no effect on the trap-nest community, and the effects of the plant diversity treatments are discussed elsewhere (Chapter 3).

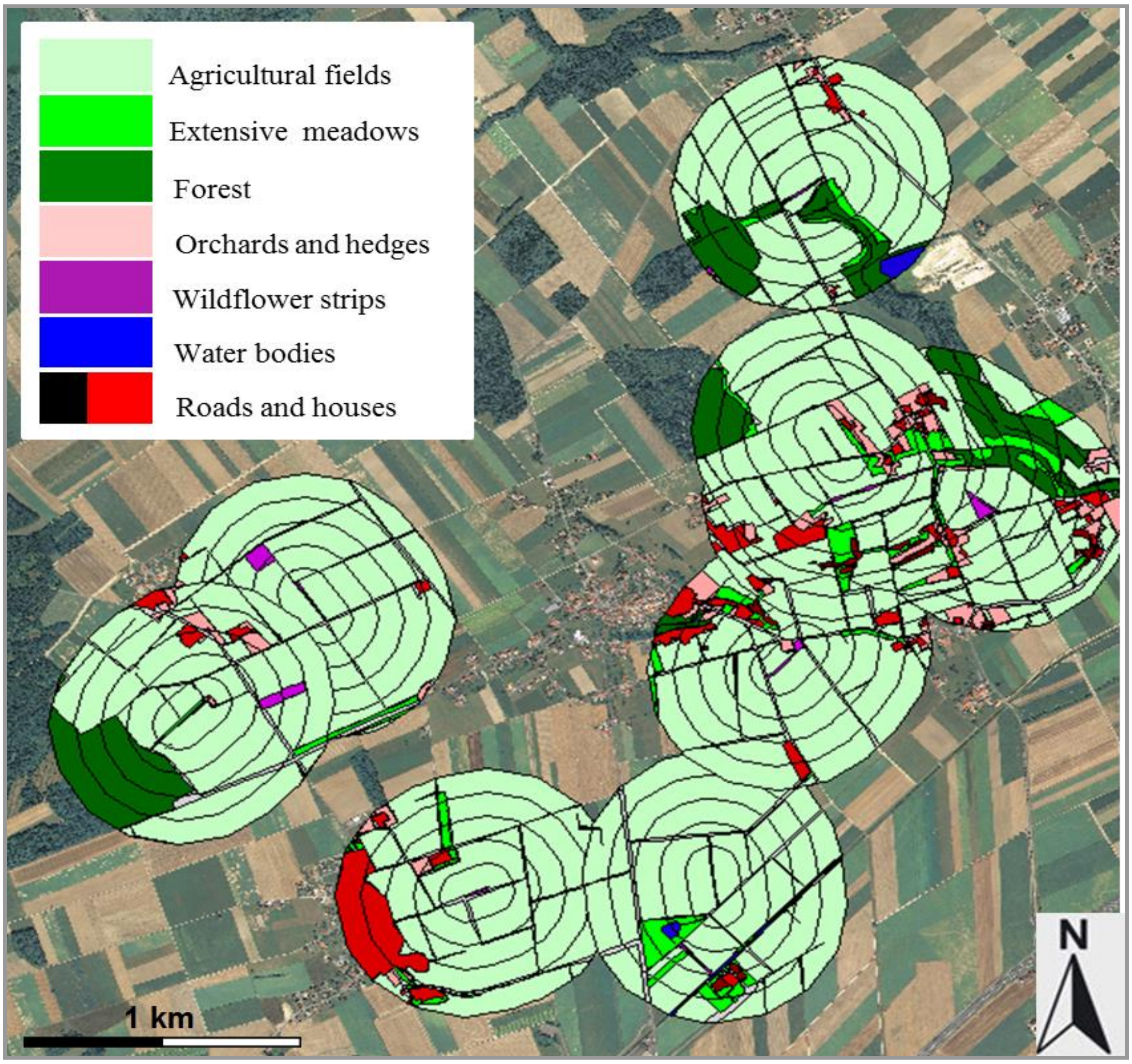


Figure S2. Aerial photo of the study area. The 10 experimental wildflower strips are surrounded by ellipsoids of 500 m radius in which land use was measured. The colours depict landscape composition.

Figure S3. Trap nests for solitary bees and wasps. Photographs show a single trap and its placement in a wildflower strip in an agricultural landscape. Fotos by N. Sandau.

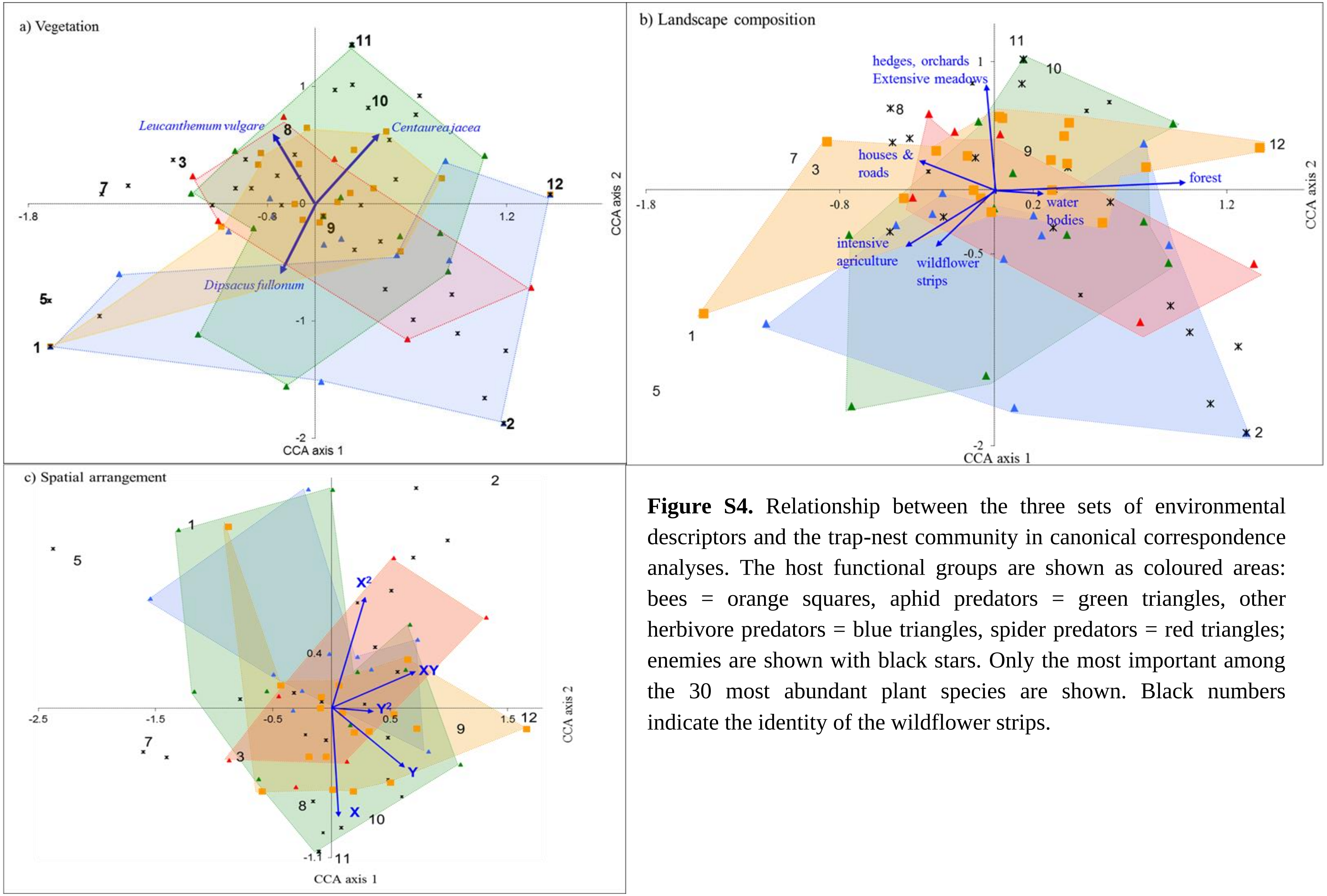


Figure S4. Relationship between the three sets of environmental descriptors and the trap-nest community in canonical correspondence analyses. The host functional groups are shown as coloured areas: bees = orange squares, aphid predators = green triangles, other herbivore predators = blue triangles, spider predators = red triangles; enemies are shown with black stars. Only the most important among the 30 most abundant plant species are shown. Black numbers indicate the identity of the wildflower strips.

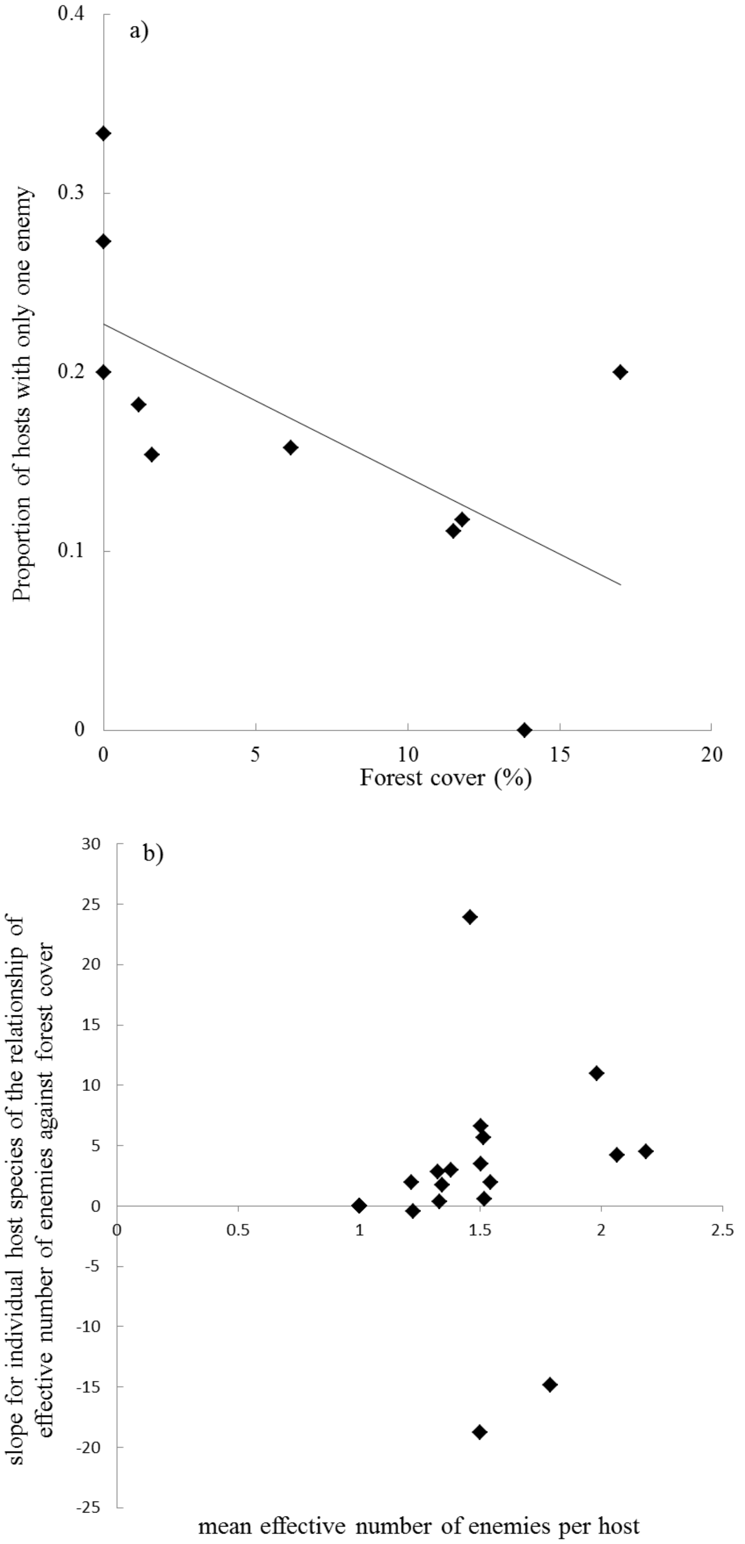


Figure S5. Potential explanations for the relationship between forest cover and vulnerability. The relationship between a) the proportion of hosts that have only a single enemy and forest cover, and b) values of the slopes for individual host species in the effective number of enemies regressed against forest cover and their mean effective number of enemies over all 10 strips. It shows that most host species interact with more enemies in strips with greater forest cover.

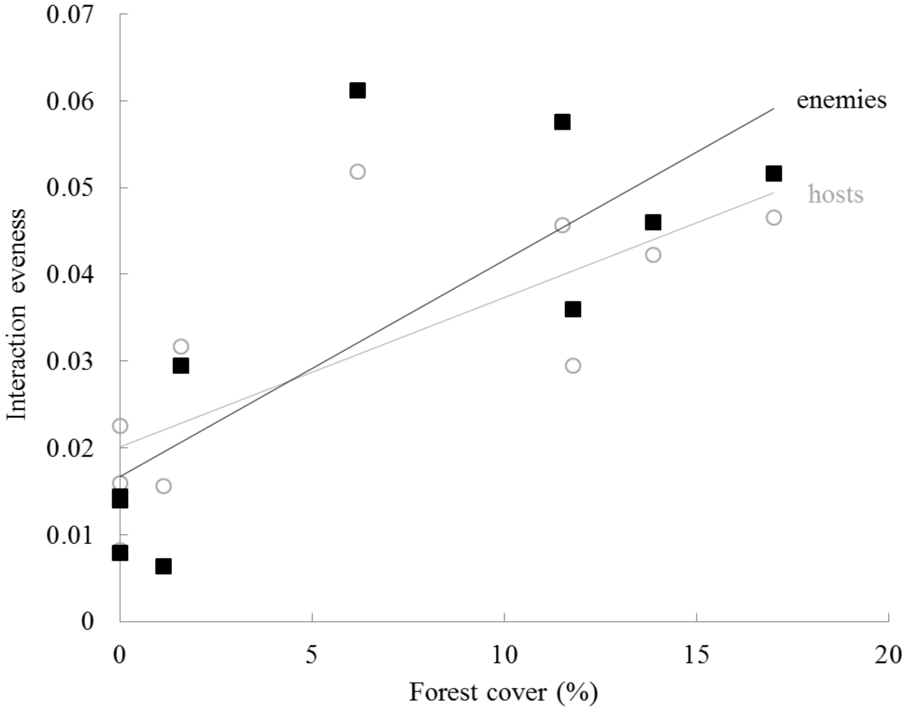


Figure S6. Potential explanations for the relationship between forest cover and generality/vulnerability: the average interaction evenness of all hosts (grey circles) and enemies (black squares) in each strip as a function of forest cover. Evenness for a given host is measured as the ratio of the Shannon index for the frequencies of interactions with its enemies, over the maximum value of this index (the log of its number of enemies). Evenness for enemies is measured similarly, but based on interactions with hosts. Values given here are averages for each food web.

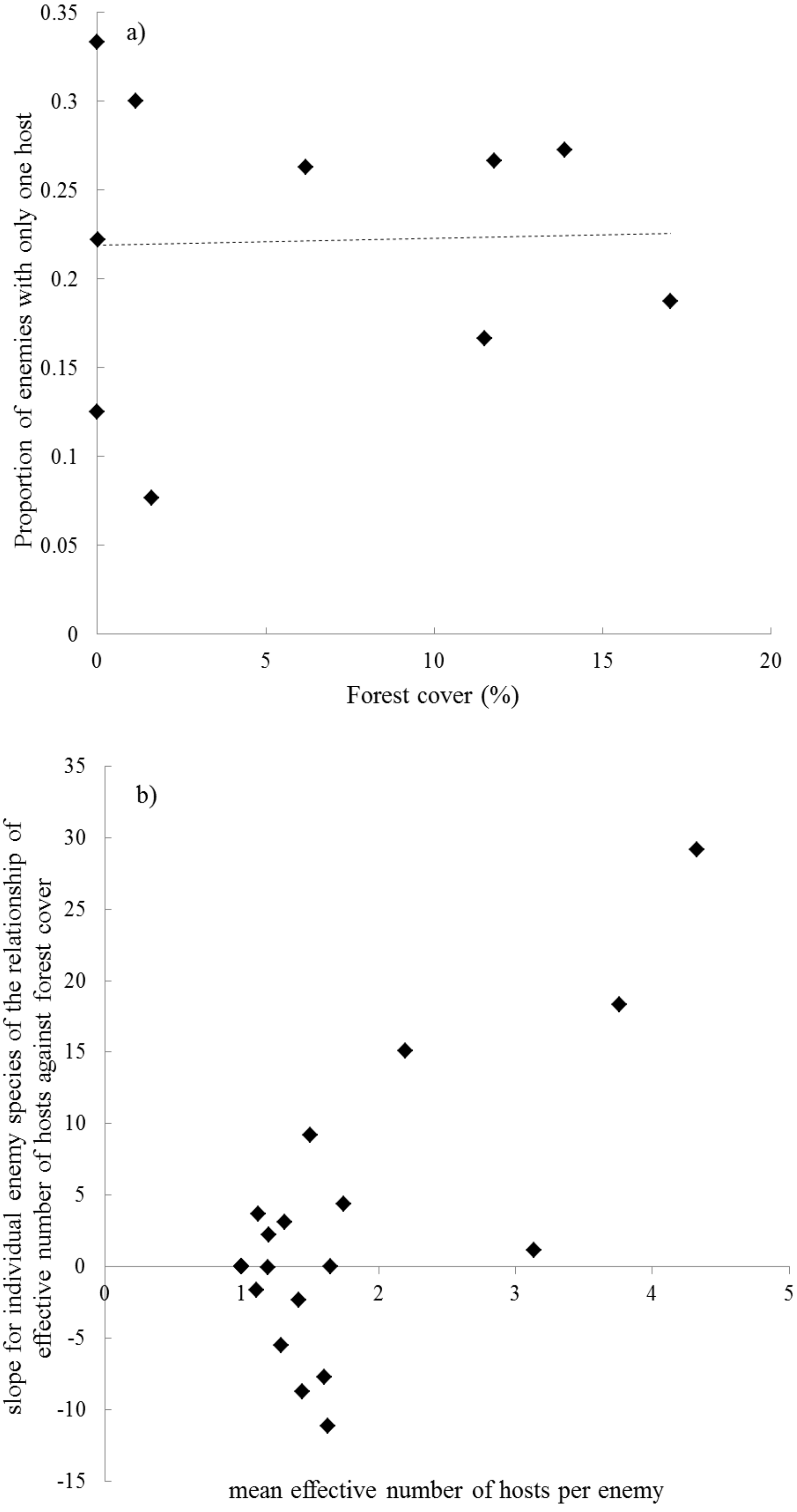


Figure S7. Potential explanations for the relationship between forest cover and generality. The relationship between a) the proportion of enemies that have only a single host and forest cover, and b) the values of the slopes for individual enemy species in the effective number of hosts regressed against forest cover and their mean effective number of prey over all 10 strips. Enemies with the highest number of hosts are also those showing the strongest positive effect of forest cover.

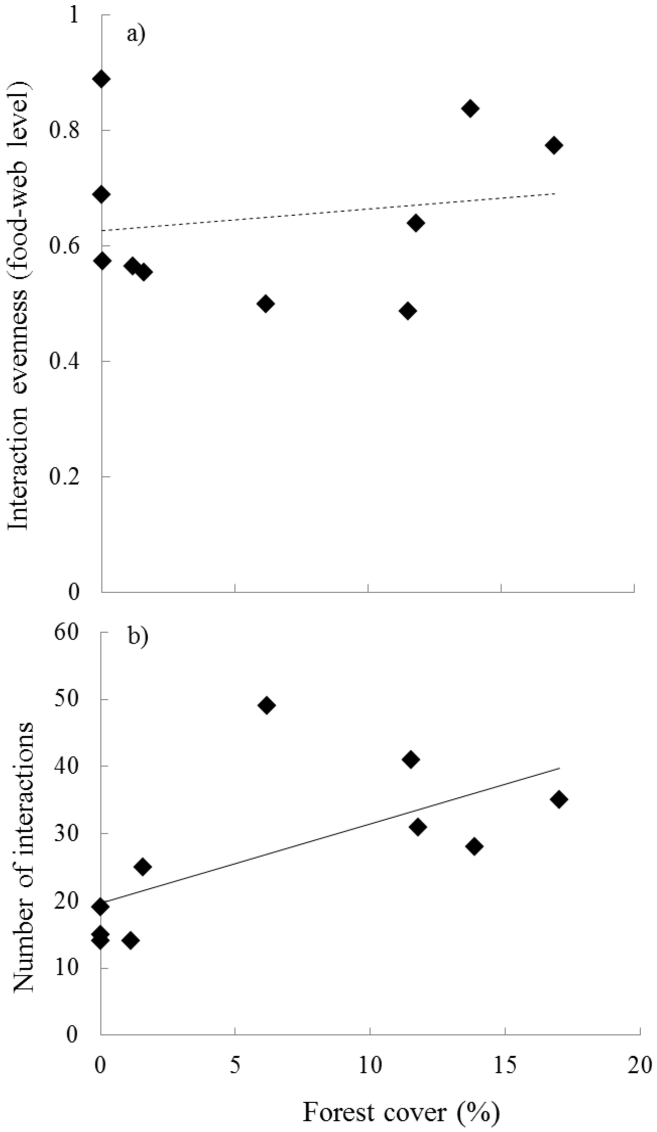


Figure S8. Potential explanations for the relationship between forest cover and interaction diversity: a) the total interaction evenness for each food web as a function of forest cover and b) the total number of interactions of each food web as a function of forest cover.

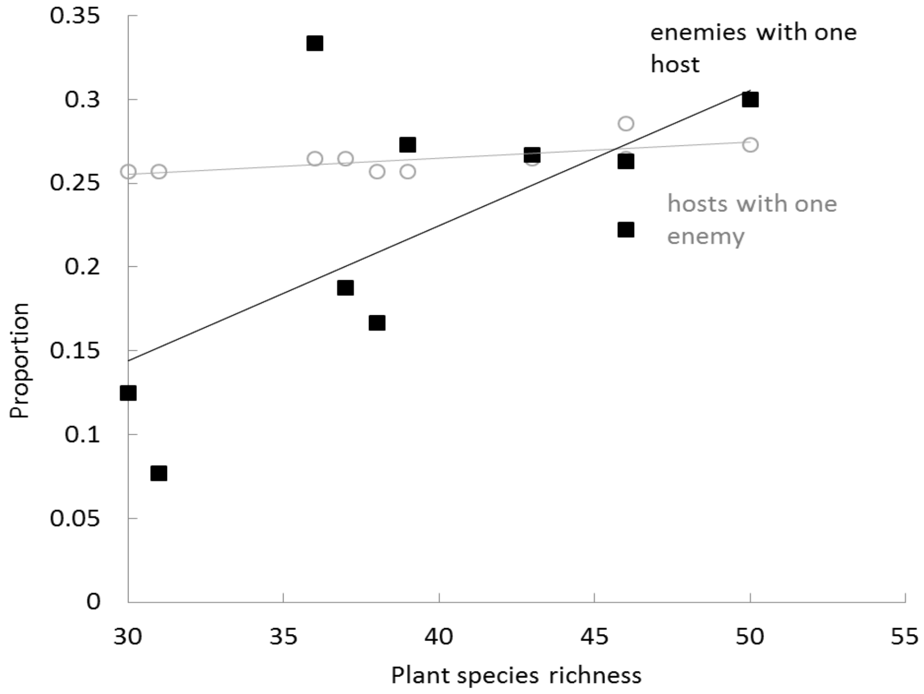


Figure S9. A potential explanation for the relationship between plant species richness and compartmentalisation: the proportion of "specialist" hosts with only one enemy (grey circles) and of specialist enemies with only one host (black squares) both increase significantly with plant species richness.

Chapter 5

Synthesis and Outlook

The general aim of our study was 1) on a small scale to compare the effect of plant diversity, structure and composition on different functional groups, of herbivorous molluscs and cavity-nesting bees, wasps and their enemies in wildflower strips, and 2) on a large scale to compare the importance of landscape composition, spatial arrangement, and vegetation on cavity-nesting bee and wasp communities and the complexity and structure of their food-webs. In the following the three different experiments will be briefly discussed and new issues raised, which were implicated by our results.

Diversity protects plant communities against generalist molluscan herbivores (Chapter 2)

In this experiment we were able to show that plant diversity has a strong negative effect on the abundance of molluscs and, *vice versa*, molluscs have a strong negative effect on plant diversity. Furthermore, plant species composition was the most important determinant of the overall composition of the gastropod community. We conclude that selective feeding by generalist herbivores leads to changes in plant community composition and hence reduced plant diversity. Thus, our study highlights the importance of plant biodiversity as protection against generalist herbivores, which if abundant can in the long term negatively impact plant diversity.

Synthesis and perspectives

The original aim of our experiment was in one plot to exclude major herbivores and their predators and in a second plot to exclude the predators. However we succeeded with the reduction of molluscs, but not of rodents. Thus, we can not exclude that some of the observed changes in plant diversity and functional group cover in the (-) mollusc plots may be partly attributed to an increased grazing pressure from rodents. In a smaller-scale experiment, beside an exclusion of molluscs, the exclusion of rodents should be possible, and the crossed effect of both herbivore groups on plant diversity and biomass could be disentangled. Through this, the relationship between plant species richness and biomass in plots with and without herbivores should be investigated (Thebault & Loreau 2003), even for a longer time than three years. In this way, it should be possible to test the prediction that generalist herbivores can change the shape of the relationship between biomass and plant diversity from linear to unimodal, with a peak in biomass at intermediate diversity.

Plant diversity in a nutshell: testing small-scale effects on trap-nesting wild bees and wasps (Chapter 3)

By implementing a correlation due to plant composition in the mixed- effect models, we were able to simultaneously analyse the effect of plant diversity, vegetation structure and composition on trap-nesting bees, wasps, their enemies, and the food web structure of these communities. Decreasing plant species richness resulted in lower wasp species richness, with significantly lower abundances of spider-predating wasps. These effects occurred on a very small scale for mobile insect species. Spider communities seemed to be regulated by a top-down effect of spider predating wasps, simultaneously with a bottom-up effect of herbivores. Surprisingly, the abundance of spiders was the only variable that was strongly affected by plant composition, with models performing better when the correlation due to plant composition was included. The quantitative and qualitative food-web metrics were neither affected by plant diversity, nor composition. We conclude that preserving even small islands of plant diversity can contribute to the conservation of biodiversity in agricultural landscapes.

Synthesis and perspectives

For flying and very mobile organisms, it is probable that resource heterogeneity at a small scale does not play a role for the choice of breeding sites. To tackle the question of the effect of plant diversity and other vegetation characteristics on bees and functional groups of wasps other than spider-predators, slightly larger wildflower areas (e.g. 10 x 20 m) could be installed, separated from each other by a distance of at least 20 m, with high, medium and low plant diversities, and with similar landscape compositions in the surroundings.

Furthermore, the identification of direct and indirect effects of vegetation composition, structure and diversity on different trap-nesting functional groups, their enemies and prey, could yield interesting results. We are currently exploring an approach based on Path analyses (Randall 2001), one form of structural equation models, which yielded promising preliminary results, but was difficult to apply due to the strong random effects of the strips. Furthermore, an identification of the provenance and diversity of the prey of trap-nesting hymenopterans could provide insights into the trophic links between compensation zones and crop plantations.

The importance of landscape and spatial structure for hymenopteran-based food webs in agro-ecosystems (Chapter 4)

On the landscape scale we were able to compare effects of vegetation, spatial arrangement and landscape composition on the trap nest communities and their food-web structure. By implementing a correlation due to the overlap of the landscape surrounding the wildflower strips in our models, we were able to account for the spatial auto-correlation between strips. Here, the landscape in the surrounding had the greatest influence, with a strong positive effect of forest cover on the diversity of the trap-nest communities and the complexity of their food webs. The system of wildflower strips therefore appears to function as a bridge between agricultural and late successional habitats, rather than behaving as a self-supporting meta-community. Besides their basic ecological interest, our results are important for the conservation of ecosystem functions and the management of agro-ecosystems.

Synthesis and perspectives

In the framework of our experimental approach, there was more variation of plant species richness between subplots of one strip than between the ten strips. Further, a higher number of replicates would yield higher statistical power to identify the effect of landscape heterogeneity and isolation on insect communities. In our study, we assumed that cavity-nesting bees and wasps provide important pollination and biological control for agricultural landscapes. However, in general there is no quantification of the ecosystem services that are really provided by these groups. Future studies using phytometers (standardized plants) with given herbivore pressure in agricultural fields close, and in various distances to wildflower strips could quantify pollination and biological control services by these groups. Further, the identification of the functional importance of different land cover types for a broad range of species and functional groups (e.g. for foraging or nesting) could be used to test the hypothesis, that functional heterogeneity is a better predictor than structural heterogeneity (Fahrig *et al.* 2011), with implications for the conservation in agro-ecosystems.

Our data could further be used to model species extinctions at different trophic levels and of different frequencies. The prediction of the effects of species extinctions, for example due to climate change, or landuse intensification, on food-web structure and stability is a contemporary issue in the pace of current global change.

GENERAL CONCLUSION

It is necessary to restore a dense network of flower-rich habitat patches in agricultural landscapes and also to conserve a diverse landscape mosaic with high proportions of woody habitat, in order to 1) ensure long-term sustainability of ecosystem services as pollination and biological control, and 2) to attract fewer, and sustain a low impact of potentially problematic herbivores. Our gained knowledge is usefull to improve current agri-environment schemes. Moreover, the study of species interactions in spatially structured meta-communities is comprehensive and global, providing results of basic ecological interests but also of relevance for conservation.

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ACKNOWLEDGEMENTS

There are many people who deserve recognition for their contributions to the results and ideas presented here.

I would like to express all my thanks to my advisor, ***Louis-Félix Bersier***, for endless patience, great ideas, and insightful feedback, and his always offered break, with a cup of coffee and Swiss chocolate. I thank you for the great time in your group!

This dissertation would not have been possible without the help and support of ***Russel Naisbit***, I have to thank you a thousand times, for your incredible endurance to correct and improve my writings!

Rudolph Rohr offered valuable statistical advice and was a stable point in the statistical jungle, until the last minute, even from one of the hottest spots on earth.

I would like to thank ***Owen Petchey*** and ***Christian Lexer*** for being the experts of my thesis and reading through all these pages.

Several other ecologists provided insightful feedback on the ideas presented here. ***Patrik Kehrli***, had the idea for this project and added substantial remarks on all manuscripts. Thanks for all your support and advice!

Nadine Sandau and ***Odile Bruggisser*** provided data, worked in the strips, identified species, prepared, and dissected trap nests - during many hours. Thanks for your patience and all what we shared! I also thank ***Alex Aebi***, for his work in the field and fruitful comments in science and life. ***Jaques Studer***, and ***all farmers*** for the realization, and the great support of this project. ***Felix Amiet, Bruno Baur, Martin Schmidt-Entling*** and ***Seraina Klopfstein*** for their kind help in wasp identification. ***Stefan Suter*** kindly taught me to catch and identify dragon-flies in the field. ***Silvie Rotzetter, Valentine Renevey, Guillaum Kuhn*** and ***Ludwika Sygnarski*** had the incredible patience to sort massive D-vac and Pitfall samples. I am honestly indepted to you.

Thanks to all the people, sharing coffee breaks and discussions during these years! Especially my office mates ***Sven Bacher*** and ***Gwenael Jacob***, who helped out with any question about computers, statistics, ecology and life. ***Christine,*** and ***Svein Haaland*** for their encouragement and an open ear any time.

Special thanks to my Capoeira, climbing, skiing and “just” friends and especially to: ***Monica Aceti, Franziska Bundi, Claudine Carett, Claudia Frey, Dorothea Lindke, Sandrine King, Maluco, Sina Schneider, Lisa Wyss, Loic Voillat*** and ***Jean-Christoph Zulian***. Your friendship and energy supported me during all these years! I had a great time in the mountains with ***Tad Kawecki***, and hope we can climb one, soon again! Thanks, a thousand times!

David Frey and ***Johanna Voigt*** were the best flat mates, and friends; thanks a lot for all your patience with the kids, and me!

Personally, I would like to thank many family members and friends who supported me in many ways during these years. First and foremost, my partner ***Till Sander***, who has continually demonstrated love, and tireless encouragement throughout our time together; I am most deeply indebted to you. I would like to thank ***Sabine, Rakuna, Eike, Anne, Gerti & Günter Sander*** and ***Hans Fabian*** for all their thoughts, ideas, photos, help and support with anything else then work, during my long education.

And last but not least, I thank you people of the ***Ecology & Evolution*** unit: ***Joao Amaral, Philipp Arnold, Thelma Barbara, Thomas Clerc, Robin Collins, Catherine Cuennet, Markus Gallus, Min Hahn, Patrik Mraz, Anne-Catherine Pasche, Nilgün Sailer, Gregoir Schaub, Alain Werro, Isabelle Zaugg,***….. and all I forgot to mention here. Thank you for your help in the field, with technical problems, and for all the fruitful discussions about, or not about science.

Thank you all!

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2. Education

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1997 - 2006	**Studies of Biology** at the Friedrich-Schiller University Jena, Germany Main subject: Ecology, subsidiary subjects: Behavioral physiology and Zoology
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3. Further professional background

2010 - 2012	**Leader** of school excursions to the Auried Nature reserve in the canton Fribourg for PRONATURA
2009 - 2011	**Co-supervisor** of three Bachelor students
2009	**Supervisor** for the Institutes' intern Writing Club for PhD and Master students
2007 - 2010	**Supervisor** of Institutes' intern Journal Club, obligate to Master students
2003	S**cientific assistant** at the CSIRO in Canberra/Australia, Investigations of time activity adjustments of bushrats (*Rattus fuscipes*) to fox activity
2001	S**cientific assistant** at the Institute of Low Temperature at Hakodate University, Sapporro, Japan, with Prof. AJ Davis Studying the ecology of mycophagous *Drosophila* diversity
2001-2003	S**cientific assistant** in ecological research at the University of Jena and the Max-Planck-Institute of Biogeochemistry

4. Workshops and courses

2012 January	Bayesian population analysis using WinBUGS
2010 June	Exploring biological networks
2009 November	Effective public speaking
2009 October	Spatial Analysis and GIS
2008 April	Introduction to Field Animal Experimentation
2008 y	Mollusc ecology, determination and systematics course

5. Publications

Fabian Y, Sandau N, Bruggisser OT, Aeby A, Kehrli P, Rohr RP, Naisbit R and Bersier LF, Diversity protects plant communities against generalist molluscan herbivores; *Ecology and Evolution* (2012), 2460-2473, doi: 10.1002/ece3.359

Bruggisser OT, Aebi A, Fabian Y, Kehrli P, Sandau N, Blandenier G & Bersier LF, Bottom- up and top-down control of *Argiope bruennichi* (Araneae: Araneidae) in semi-natural ecosystems, *Journal of Basic and Applied Ecology* (2012), 13, 706-714.

Fabian Y, Sandau N, Bruggisser OT, Aeby A, Kehrli P, Rohr RP, Naisbit R and Bersier LF, The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem (in revision in *Journal of Animal Ecology*)

Fabian Y, Sandau N, Bruggisser OT, Aeby A, Kehrli, P, Rohr RP, Naisbit R and Bersier LF, Plant diversity in a nutshell- testing for small-scale effects on trap nesting wild bees and wasps (submitted to *Ecosphere*)

Fabian Y, Sandau N, Bruggisser OT, Naisbit R , Aeby A, Kehrli P and Bersier LF, Carabid abundance and diversity in experimentally manipulated wildflower strips – The role of plant diversity for predators (in preparation)

Bruggisser OT, Aebi A, Fabian Y, Kehrli P, Sandau N, Blandenier G & Bersier LF, Spider molecular barcode to track trophic links in bioindicator food webs (in preparation)

Sandau N, Rohr RP, Naisbit R, Fabian Y, Bruggisser O, Aeby A, Kehrli, P & Bersier LF Including community composition in biodiversity-productivity models (submitted to *Ecology Letters*)

Fabian Y, (2006) Foraging behaviour of Argentine ants (*Linepithema humile*) and other resident ant species in relation to resource density and distribution: implications for competitive interactions and coexistence, Diploma Thesis at the University of Jena

6. Conference presentations

Fabian Y, Sandau N, Bruggisser O, Aeby A, Kehrli, P, Rohr RP, Naisbit R & Bersier LF (2013) The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem, PACE 2013, Basel, Switzerland (Talk)

Fabian Y, Sandau N, Bruggisser O, Naisbit R & Bersier LF (2012) The importance of plant diversity, landscape composition and wildflower strip spatial distribution on a bee and wasp metacommunity, Biology12, Fribourg, Switzerland (Talk)

Fabian Y, Sandau N, Bruggisser O, Naisbit R and Bersier LF (2010) The effect of plant diversity on a hymenopteran based food-web, British ecological society Conference Leeds England (Poster)

Fabian Y, Sandau N, Bruggisser OT, Naisbit R and Bersier LF (2010), Diversity protects plant communities against generalist herbivores Biology10 Neuchatel, Switzerland (Poster)

Fabian Y, Bersier LF (2009), Species abundance patterns in food webs, Biology09 Bern, Switzerland (Poster)

Fabian Y, Clerc T & Bersier LF, (2008) Species abundance and trophic structure in food webs, British ecological society Conference London England (Talk)

Aebi A, Bruggisser OT, Fabian Y, Sandau N and Bersier LF (2007), Wildflower Strips in a Network: A Meta-Community Approach, SWIFCOB Bern, Switzerland (Poster)

EHRENWÖRTLICHE ERKLÄRUNG

Ich erkläre hiermit ehrenwörtlich, dass ich die folgende Arbeit mit dem Titel: „*Insect and mollusc communities in wildflower strips: Effects of plant diversity and surrounding landscape in an argo-ecosystem*“, entsprechend den Regeln guter wissenschaftlicher Praxis selbstständig und ohne unzulässige Hilfe Dritter angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommenen Gedanken, sowie sämtliche von anderen, direkt oder indirekt übernommenen Daten, Techniken und Materialien sind als solche kenntlich gemacht. Die Arbeit wurde bisher bei keiner anderen Hochschule zu Prüfungszwecken eingereicht.

Fribourg, 16.11.2012

Yvonne Fabian