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Landscape context and elevation affect pollinator communities in intensive apple orchards

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Abstract

Although an extensive research has been done on the contribution of wild insects to apple pollination, most of these studies did not evaluate the effect of the surrounding landscape context on local pollinator communities. Our aim was to compare communities of wild bees in 31 equally managed apple orchards located in three contrasting landscape types (either dominated by apple, forest, or grasslands) and along an elevation gradient and to test a potential interaction between landscape context and elevation. The study was carried out in 2009 in Trentino (NE Italy), one of the major apple growing areas of Europe with ∼12,000 ha of commercial orchards distributed between 150 and 950 m a.s.l. We found that apple-dominated landscapes drastically reduced wild bee species richness and abundance in the orchard compared to landscapes dominated by either grassland or forest. Forest-dominated landscapes benefited local species richness more than grassland-dominated landscapes, while abundance did not differ between grassland and forest. Total species richness and abundance further declined with increasing elevation, while no interactive effect was found between temperature and landscape context. The abundance of *Apis mellifera* in the apple-dominated landscapes was two to four times higher than in the landscapes dominated by forest and grasslands, respectively. Measures to restore natural pollinator communities by providing suitable habitats around the orchard would not only benefit conservation of general biodiversity, but would probably also contribute to reduce the dependence of apple pollination on managed honey bees.

Zusammenfassung

Obwohl weitreichende Forschungen über den Beitrag von Wildinsekten zur Apfelbestäubung durchgeführt wurden, haben die meisten dieser Studien nicht den Einfluss der umgebenden Landschaft auf die lokalen Bestäubergemeinschaften bestimmt. Unser Ziel war es, die Wildbienengemeinschaften von 31 gleichartig bewirtschafteten Apfelplantagen, die in drei unterschiedliche Landschaftstypen (dominiert von Apfel, Wald oder Grasland) eingebettet waren und einen Höhengradienten repräsentierten, zu vergleichen und die potentielle Interaktion zwischen Landschaftskontext und Höhenstufe zu testen. Die Untersuchung wurde 2009 im Trentino (Nordost-Italien) durchgeführt, einem der bedeutendsten Apfelanbaugebiete Europas, in dem rund 12.000 ha

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kommerzieller Apfelplantagen zwischen 150 und 950 m ü. NN verteilt liegen. Wir fanden, dass Apfel-dominierte Landschaften Artenreichtum und Abundanz der Wildbienen in der Plantage drastisch verringerten verglichen mit Wald- oder Grasland-dominierten Landschaften. Eine Wald-dominierte Umgebung förderte den Artenreichtum mehr als die Dominanz von Grasland, während sich für die Abundanz kein Unterschied ergab. Die Gesamtartenzahl und die Abundanz gingen mit zunehmender Höhe zurück, während keine Interaktion zwischen Temperatur und Landschaftskontext gefunden wurde. Die Abundanz der Honigbiene war in den Apfel-dominierten Landschaften zwei- bis viermal höher als in den Wald- bzw. Grasland-dominierten Landschaften. Maßnahmen zur Wiederherstellung von natürlichen Bestäubergemeinschaften durch Bereitstellung geeigneter Habitate in der Umgebung der Plantagen würden nicht nur die Bewahrung der Biodiversität im Allgemeinen fördern, sondern wahrscheinlich auch dazu beitragen, die Abhängigkeit der Apfelbestäubung von bewirtschafteten Honigbienen zu verringern.

Keywords: *Apis mellifera*; Climate; Grassland; Forest; Fruit tree; Honey bee; Pesticide; Pollination; Semi-natural habitat; Wild bees

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Introduction

The presence of semi-natural habitats in the landscape surrounding farms has important positive effects on pollinator diversity and pollination service in various crops (Garibaldi et al. 2012). The majority of crops included in recent landscape studies are herbaceous species and less attention has been paid to the effect of landscape context on pollinators visiting important perennial crops (but see Steffan-Dewenter 2003; Watson, Wolf, & Ascher 2011; Holzschuh, Dudenhöffer, & Tscharntke 2012). Although there is a large body of research investigating the contribution of wild insects to apple pollination (e.g. Atwood 1933; Kendall 1973; Thomson & Goodell 2001; Sheffield, Smith, & Kevan 2005; Gardner & Ascher 2006), most of these studies have not considered the effect of landscape context on pollinator communities visiting the orchards during bloom (but see Watson et al. 2011). Apple is an important crop globally and plantations are often intensively cultivated covering large areas. These monoculture landscapes are expected to be an unsuitable habitat for many wild pollinator species due to the intensive inputs of agrochemicals, low forage resources, and lack of nesting sites (Scott-Dupree & Winston 1987; Alston et al. 2007; Sheffield, Kevan, Westby, & Smith 2008). Although in most cases apple pollination is effectively delivered by moving *Apis mellifera* hives into the orchards, several wild bee species are also effective pollinators of apple and on an individual basis tend to be better pollinators (Kendall 1973; Thomson & Goodell 2001). Recent declines in the number and survival of *A. mellifera* colonies suggest that it is important to investigate to what extent different semi-natural habitats surrounding the crop can provide wild bee populations that may replace or complement *A. mellifera* in crop pollination (NRC 2007; Watson et al. 2011).

Besides land-use intensification, climate is expected to strongly affect insect distribution and activity (Kevan & Baker 1983). Although many crops such as apple are grown in very different climatic regions and along relatively wide elevation ranges, no studies have simultaneously investigated possible interactive effects on pollinator communities of land-use intensification in contrasting climates. In terms of relative species richness for different taxa, hymenopterans are generally the dominant pollinators in low-elevation communities, while lepidopterans or dipterans usually dominate the pollinator fauna at higher elevations (Arroyo, Kalin, Primack, & Armesto 1982). These findings lead to the expectation that crops that are highly bee-dependent, such as apple, are more pollinator-limited when growing at high rather than at low elevations. Because pollinator taxa differ in their sensitivity to land-use change (Bommarco et al. 2010) and in response to temperature, understanding a potential interaction between the two factors may provide important implications for pollinator diversity conservation.

In this study, we compared the wild bee communities in 31 equally intensively managed apple orchards in one of the major apple growing areas of Europe. The orchards were situated in landscapes with different proportions of crop and non-crop areas and located along an elevational gradient. The first aim was to examine how species richness and abundance of bees found in the orchards during bloom varied depending on three types of surrounding landscape; either dominated by the apple crop, semi-natural forest, or grasslands. We hypothesize that the intensively managed apple orchard is an unsuitable habitat for most wild bee species due to the intensive use of agrochemicals and low floral resources (Thompson 2001; Alston et al. 2007; Tuell & Isaacs 2011), and that higher cover of either grassland or forest in the surrounding landscape will therefore enhance local diversity and abundance of wild pollinators. A second aim was to test potential negative synergies between elevation-related cold temperatures and landscape. We expect that increasing elevation will be associated with a decrease of wild bee species richness and abundance due to the negative effect of cold temperatures.

Materials and methods

Study area

The study was carried out in 2009 in four neighbouring administrative districts of the Trento Province in NE Italy: Low Valsugana, High Valsugana, Val Lagarina, and Val di Non. The study area covered about 1250 km^2 in the Southern

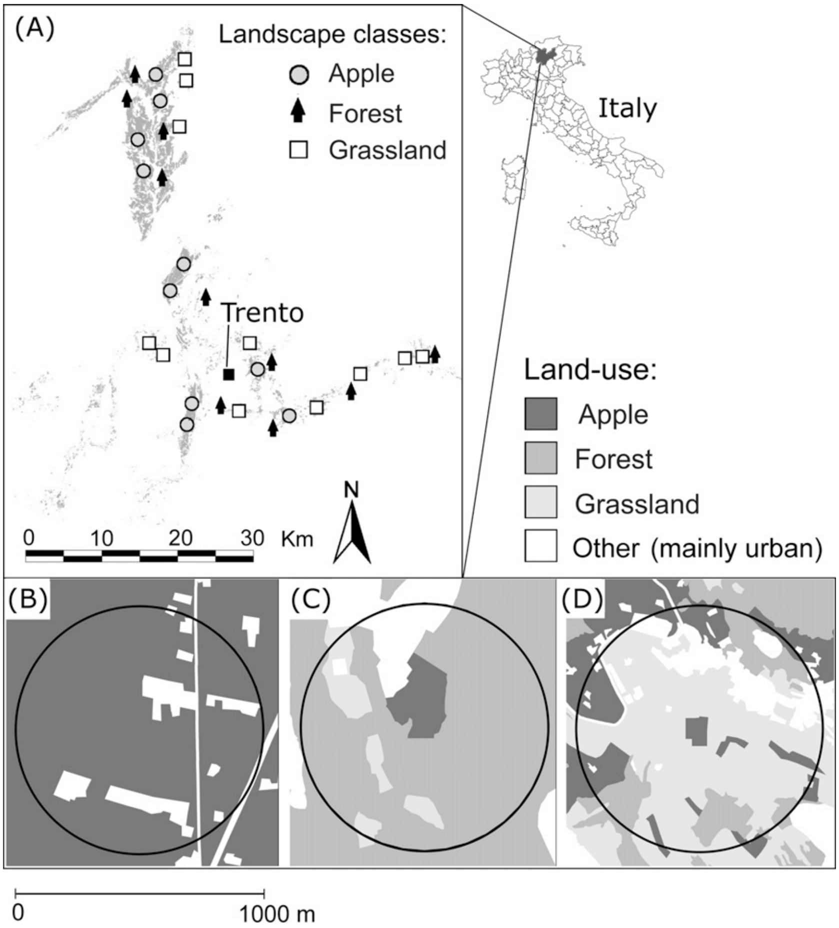

Fig. 1. Location of the 31 apple orchards sampled in the Trentino region (NE Italy) and classified into our three landscape classes (A). The grey-shaded area indicates the coverage of apple orchards in the region. In the three panels below examples of landscape classes are shown: (B) apple-dominated, (C) forest-dominated, and (D) grassland-dominated landscapes.

European Alps. The mean annual temperature was ~13.5 °C at 150 m, ~8.5 °C at 1000 m elevation and the mean annual rainfall varied between 950 and 1050 mm throughout the region.

The study region is one of the major apple growing areas of Europe with ~12,000 ha of intensive, commercial orchards distributed between 150 and 1000 m. Management is highly specialized and homogenous in the whole study area with only very few organic or traditionally managed orchards. In the last decades, there has been a dramatic landscape homogenization that has created large areas covered exclusively by apple orchards (up to ~10 km × 10 km). However, it is still possible to find some scattered orchards located in a non-crop matrix composed of grasslands and forests. In the area, grasslands are usually heavily fertilized (>200 kg N ha^{-1} yr^{-1}) and mown 2–4 times per year (depending on elevation) resulting in dense swards dominated by grasses and with low forb abundances (see Marini, Scotton, Klimek, & Pecile 2008). Forests are mainly composed of Scots pine mixed with broad-leaf tree species (mainly *Fraxinus ornus* L. and *Ostrya carpinifolia* Scop.).

Sampling design

Thirty-one integrated commercial apple (*Malus* × *domestica* Borkh.) orchards with the variety 'Golden Delicious' were selected in landscapes characterized by different proportions of crop and non-crop habitats (Fig. 1). We selected 10 orchards in landscapes dominated by apple plantations, 10 in landscapes dominated by forests and 11 in landscapes dominated by grasslands (Table 1). The three habitats represent the main land uses in the region. We identified sites embedded in the three landscape classes by quantifying landscape composition within a 500 m radius around each selected orchard using detailed land-use maps (Servizio Urbanistica, Pronvincia di Trento) in ArcGIS 10 (ESRI®). For each selected orchard, we further quantified the cover of apple, forests and grasslands at four nested spatial scales (250, 500, 1000, and 2000 m radius) to assess the consistency of the landscape classes when measured among spatial scales. Except for the 2000 m radius, where forest tended to increase in all the three landscape classes, the relative proportion of the three habitats remained more

Table 1. Landscape and local information (with mean and standard deviation in parenthesis) recorded in the 31 apple orchards located in the three landscape composition classes.

	Landscape composition classes			P^a
	Apple ($n = 10$)	Forest ($n = 10$)	Grassland ($n = 11$)	
Local variables				
Annual mean temperature (°C)	11.30 (1.9)	10.46 (0.72)	10.43 (0.96)	0.10
Elevation (m a.s.l.)	464(252)	601(147)	609(216)	0.23
Slope (%)	4.5 (5.8)	12.6 (4.7)	6.0 (5.1)	**<0.01**
Size of the orchard (area within a 100 m radius buffer) (ha)	30.7 (1.1)	16.8 (6.5)	12.1 (7.7)	**<0.01**
Landscape variables (250 m radius buffer)				
Cover of apple (%)	94.1 (5.8)	19.1 (9.4)	13.9 (9.3)	**<0.01**
Cover of forest (%)	0.12 (0.4)	69.4 (12.3)	7.4 (11.3)	**<0.01**
Cover of grassland (%)	0.50 (1.6)	7.6 (11.7)	71.0 (14.6)	**<0.01**
Landscape variables (500 m radius buffer)				
Cover of apple (%)	85.0 (11.7)	12.2 (7.5)	12.6 (9.1)	**<0.01**
Cover of forest (%)	2.1 (9.3)	73.4 (8.1)	11.1 (10.9)	**<0.01**
Cover of grassland (%)	2.1 (2.1)	10.2 (9.6)	65.7 (12.5)	**<0.01**
Landscape variables (1000 m radius buffer)				
Cover of apple (%)	70.3 (8.8)	15.9 (17.8)	12.5 (5.6)	**<0.01**
Cover of forest (%)	11.4 (8.6)	67.7 (15.7)	28.4 (16.0)	**<0.01**
Cover of grassland (%)	6.3 (5.7)	9.8 (10.0)	47.0 (13.8)	**<0.01**
Landscape variables (2000 m radius buffer)				
Cover of apple (%)	47.6 (11.6)	19.3 (16.1)	10.1 (5.6)	**<0.01**
Cover of forest (%)	31.0 (8.8)	60.8 (15.8)	46.5 (18.4)	**<0.01**
Cover of grassland (%)	5.16 (6.8)	9.6 (9.2)	40.3 (11.3)	**<0.01**

Bold values are significant at $P < 0.05$.

[a] P-value from a one-way ANOVA F-tests.

or less stable at all other spatial scales (Table 1). The scales were chosen to be similar to the range of foraging distances of wild bees (Gathmann & Tscharntke 2002). For each landscape class, we selected orchards with the same local management and located at elevations between 150 and 950 m such that the elevation did not differ among the three landscape classes (Table 1). For each orchard, we measured elevation and slope and we used interpolated climatic data to derive mean annual temperature by averaging values over the period 1990–2000 (Sboarina & Cescatti 2004). As orchards belonging to different farmers are often embedded in a continuous monoculture landscape, the actual size of the orchard in which samples were taken was not expected to have an effect on insect communities. Preliminary analyses including orchard size in the models showed that this factor was never important. We therefore did not include this variable.

Local management

Orchards were selected to keep local management constant as much as possible and to test for the effect of surrounding landscape, elevation, and their interaction, on wild bee species richness and abundance. All orchards were of similar age and management history and were currently managed in a similar way under integrated pest management (IPM). To control pests, various classes of pesticides were used including insect growth regulators, organophosphates, carbamates, Spinosad, and neonicotinoids. The number of insecticide applications under IPM varied between five and six in all orchards in 2009 and did not differ between the three landscapes classes. Insecticide applications usually started in March and ended in August and were suspended during the flowering period to avoid direct mortality of domesticated and wild bees.

Insect sampling

Wild bees (Hymenoptera: Apoidea) and *A. mellifera* were sampled only during the apple flowering period between 18 April and 4 May 2009. The aim of our sampling was to identify which semi-natural habitat in the landscape provides the largest contribution of wild pollinators visiting the orchard. We used a passive sampling with pan-traps (350 ml plastic bowl) painted with UV-bright colour to enhance efficiency (Westphal et al. 2008). We used only white pan-traps as we were interested in sampling wild bees potentially visiting white flowers. Within each orchard, 15 pan traps were placed in five clusters with three traps in each cluster. The five clusters were separated by about 7 m. Within a cluster, the three pan traps were mounted on a wooden pole at 0.8 m height, and were filled with water and a drop of detergent (2% dilution). Sampling was always done under stable sunny weather. During the flowering period, three catch-rounds were conducted with the pan traps (each time for 24 hours) for a total of 72 hours of sampling per each site. Because orchards bloomed at different times, we standardized the sampling period using the bloom phenology, i.e. the trapping started when half of the flowers were open and ended before petals started to fall on the ground.

Data analysis

We used generalized linear models to test the effect of landscape classes, elevation, and their interaction on species richness and abundance of wild bees. We employed a Poisson-distribution with log-link function for species richness, and a normal distribution with identity link function for ln-transformed total species abundance. We ran the analyses for all the species together (excluding *A. mellifera*) and separately for the following groups of species: andrenid bees (Hymenoptera: Andrenidae), halictid bees (Hymenoptera: Halictidae), bumble bees (Hymenoptera: Apidae: Bombus spp.), and mason bees (Hymenoptera: Megachilidae: Osmia spp.), and *A. mellifera*. Analyses were performed using the glm(stats) and lm(stats) functions in R version 2.12.0 (R Development Core Team 2011).

Results

Overall, in the 31 apple orchards we caught 875 individuals 345 of which were *A. mellifera.* We found 25 bee species and 14 additional clearly distinguishable morphospecies (Hymenoptera: Apoidea) of which two were anthophorid, 10 andrenid, nine bumble bee, 12 halictid, and six mason bee species (see Appendix A). Except for mason bees, which are cavity-nesting, all the others are ground-nesting species. The three most abundant species were *A. mellifera*, *Lasioglossum morio* (Fabricius) and *Andrena dorsata* (Kirby), which accounted for 40%, 33%, and 6% of the total catch, respectively.

Both the surrounding landscape and elevation had an effect on total wild bee species richness and abundance, while the interaction between elevation and landscape was never significant (Table 2). Overall, the landscapes dominated by forests supported the highest number of wild bee species, followed by the grassland-dominated landscapes, while the landscapes dominated by apple orchards supported the fewest number of species (Fig. 2A). When the species groups were analyzed separately, we found some differences in the response. Andrenid bee richness was highest in forest, intermediate in grasslands and lowest in apple (Fig. 2B). Bumble bee species richness was highest in the forest-dominated landscape, but was equally low in apple- and grassland-dominated landscapes (Fig. 2C). Halictid bee species richness was relatively higher and similar in forest- and in grassland-dominated landscapes and lower in the apple-dominated landscapes (Fig. 2D). Finally, mason bee species richness did not differ among the three landscapes types (Fig. 2E). We generally found similar patterns of species abundance (Fig. 2F), although the difference between forest and grassland landscapes was less marked. These results were due to the relatively high density of *L. morio*, *Andrena dorsata*, and *Andrena haemorrhoea* (Fabricius) in the grassland landscapes (see Appendix A). We also found some differences in abundance between species groups. Andrenid bees were only slightly more abundant in the forest compared to the grassland landscapes (Fig. 2G). Bumble bee and halictid bee abundance were like those for total species richness, although significance levels differed (Fig. 2H and I). For mason bees we found higher abundance in the forest-dominated landscapes as compared to both apple- and grassland-dominated landscapes (Fig. 2J). Total species richness and abundance declined with elevation (Fig. 3). This effect was evident only for halictid and mason bees, while andrenid bees and bumble bees did not show any relationship with elevation (Table 2). The abundance of *A. mellifera* in the apple-dominated landscapes was two to four times higher than in the landscapes dominated by forest and grasslands respectively (Fig. 4). *A. mellifera* abundance did not vary with elevation (Table 2).

Discussion

Our study shows that intensified exploitation of the landscape through the expansion of intensive apple monoculture drastically reduced species richness and abundance of wild bees that visit apple orchards during bloom. This pattern was consistent across a wide range of elevation and associated ambient temperatures. Similarly to the findings of Watson et al. (2011) in North America, the presence of semi-natural non-crop areas around the apple orchards has been confirmed to support relatively diverse wild bee communities with population abundances comparable with that of the *A. mellifera*. The almost complete absence of wild pollinators during apple bloom in the most intensively cultivated landscapes has induced many farmers to implement a coordinated pollination management based on the translocation of honey bee hives.

The reduced bee species richness and abundance within the orchard-dominated landscapes can be probably explained by the relatively high level of agrochemicals under IPM, and the lower forage resources compared to the non-crop habitats (Scott-Dupree & Winston 1987; Sheffield, Kevan, Westby, et al. 2008). Although the level of pesticide applications in the region is relatively low compared to other European growing areas (Pesticide Action Network 2007), many pesticides and also fungicides are known to be toxic to bees and pose a substantial risk if they are used extensively (Thompson 2001; Richards & Kevan 2002; Ladurner, Bosch, Kemp, & Maini

Table 2. Results from the generalized linear models testing effects of three landscape classes (apple, forest, and grassland) and elevation on species richness and abundance. GLMs were performed using a Poisson distribution (log-link function) for species richness, and a normal distribution (identity-link function) for ln-transformed species abundance. Both total species richness and abundance did not include *A. mellifera*. As the interaction between elevation and landscape was never significant ($P > 0.10$), we removed it from all the models.

	Species richness				Abundance			
	Estimate[a]	SE	z	P	Estimate[a]	SE	t	P
(a) Total								
(Intercept)	0.480	0.381	1.26	0.208	1.9632	0.4137	4.75	**<0.001**
Landscape(Forest)	2.177	0.350	6.22	**<0.001**	2.4324	0.3668	6.63	**<0.001**
Landscape(Grassland)	1.602	0.360	4.46	**<0.001**	2.0807	0.3606	5.77	**<0.001**
Elevation	−0.001	0.001	−2.10	**0.036**	−0.0025	0.0007	−3.46	**0.002**
(b) Andrenid bees								
(Intercept)	−0.938	0.678	−1.38	0.166	0.6881	0.4623	1.49	0.148
Landscape(Forest)	2.486	0.617	4.03	**<0.001**	1.7934	0.4100	4.38	**<0.001**
Landscape(Grassland)	1.729	0.639	2.71	**0.007**	1.4018	0.4030	3.48	**0.002**
Elevation	−0.001	0.001	−0.72	0.471	−0.0009	0.0008	−1.13	0.267
(c) Bumble bees								
(Intercept)	−2.820	1.224	−2.30	**0.021**	−0.1068	0.2119	−0.50	0.619
Landscape(Forest)	2.441	1.046	2.33	**0.020**	0.6815	0.1879	3.63	**0.001**
Landscape(Grassland)	1.368	1.110	1.23	0.218	0.1643	0.1848	0.89	0.382
Elevation	0.001	0.001	0.78	0.438	0.0004	0.0004	1.04	0.306
(d) Halictid bees								
(Intercept)	0.274	0.524	0.52	0.601	1.6925	0.4815	3.52	**0.002**
Landscape(Forest)	1.429	0.508	2.82	**0.005**	1.9760	0.4270	4.63	**<0.001**
Landscape(Grassland)	1.367	0.496	2.76	**0.006**	1.8459	0.4198	4.40	**<0.001**
Elevation	−0.002	0.001	−2.09	**0.036**	−0.0027	0.0008	−3.26	**0.003**
(e) Mason bees								
(Intercept)	−17.460	2536	−0.01	0.995	0.2709	0.2276	1.19	0.244
Landscape(Forest)	20.130	2536	0.01	0.994	0.6977	0.2018	3.46	**0.002**
Landscape(Grassland)	18.740	2536	0.01	0.994	0.3371	0.1984	1.70	0.101
Elevation	−0.004	0.002	−2.13	**0.033**	−0.0006	0.0004	−1.49	0.147
(f) *A. mellifera*								
(Intercept)	–	–	–	–	2.754	0.420	6.560	**<0.001**
Landscape(Forest)	–	–	–	–	−0.933	0.372	−2.506	**0.018**
Landscape(Grassland)	–	–	–	–	−1.147	0.366	−3.134	**0.004**
Elevation	–	–	–	–	0.0002	0.0007	0.257	0.799

Bold values are significant at $P < 0.05$.

[a] The estimates for Landscape(Forest) and Landscape(Grassland) correspond to the differences between the mean value of the apple-dominated landscape and the forest- and the grassland-dominated landscapes, respectively.

2005; Alston et al. 2007; Brittain, Vighi, Bommarco, Settele, & Potts 2010; Kovács-Hostyánszki, Batáry, & Báldi 2011). Although pesticide applications are always suspended during bloom, many wild bee species are probably active in the orchards longer than the duration of the bloom period. This behaviour has the potential to increase lethal pesticide exposure, especially during the post-bloom period (Thompson 2001; Tuell & Isaacs 2011). Another explanation for the very low bee abundance and richness in the apple-dominated landscapes is the scarcity of nectar and pollen resources available to bees after apple bloom. In fact, crop flowering period is much shorter than the periods in which adult wild bees are active. Scarcity of forage following apple bloom may therefore reduce bee fecundity and populations' viability (Sheffield, Westby, Smith, & Kevan 2008). As a result of the processes described above, the current orchard management is probably too intensive to maintain viable populations of wild bees within the agro-ecosystem (Roulston & Goodell 2011). The size of practically continuous blocks of orchards was in some cases up to 10 km^2, vastly exceeding the average foraging distances even for some of the most mobile species (Gathmann & Tscharntke 2002). The core areas of these large blocks are thus not accessible to wild bee populations inhabiting the semi-natural habitats even if the apple bloom provides abundant and rewarding pollen and nectar resources. As already found in other perennial crops (e.g. sweet cherry, Holzschuh et al., 2012), we found a strong positive influence of semi-natural habitats in the surrounding landscapes on local wild bee communities visiting our intensive orchards. Given the low suitability of IPM orchards for bee reproduction and persistence, the relatively large number of species and individuals found in orchards located in

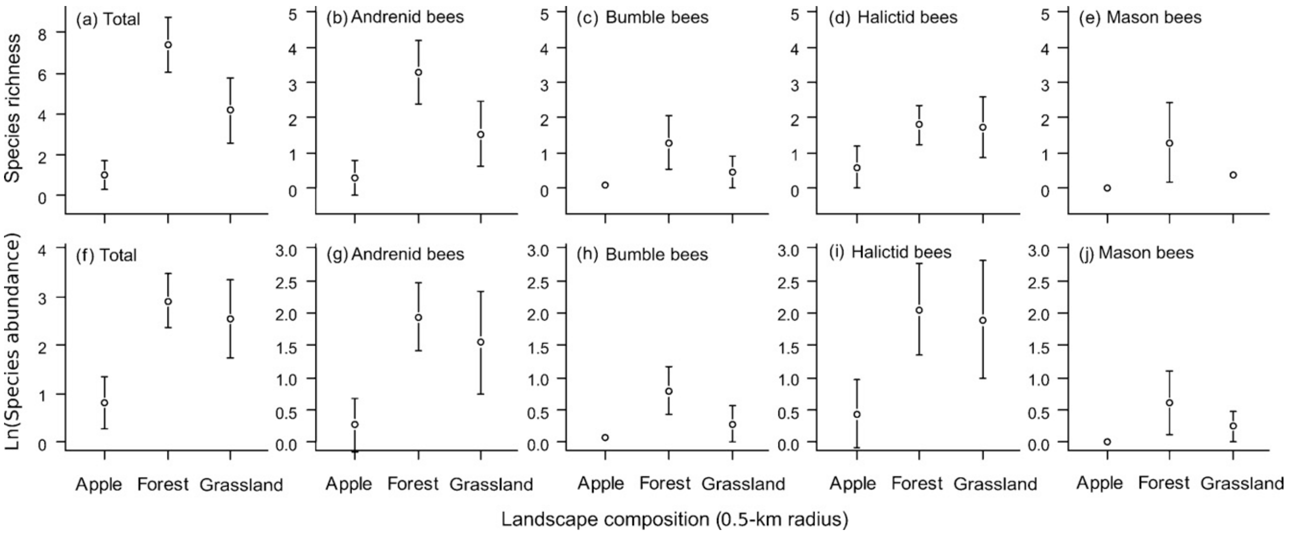

Fig. 2. Effect of landscape composition on (A–E) species richness and (F–J) species abundance (ln-transformed) of wild bees (sum per orchard). Group means and 95% confidence intervals are reported. Both total species richness and abundance did not include *A. mellifera*.

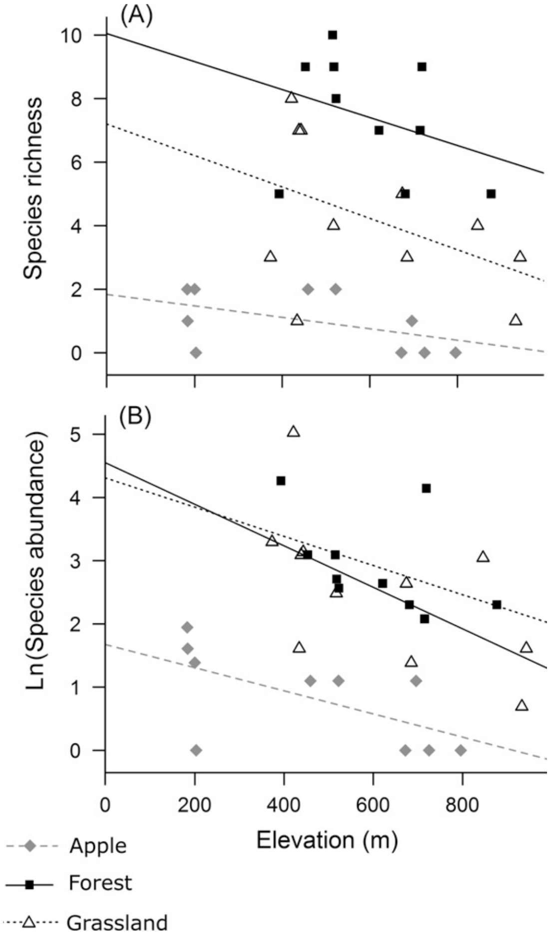

Fig. 3. Relationship between elevation and either (A) total wild bee species richness or (B) total ln-transformed bee abundance in each orchard for the three landscape classes, separately. Both species richness and abundance did not include *A. mellifera*. The fitted lines are simple linear regressions showing the relationship for the three landscape classes, separately.

landscapes with large cover of semi-natural habitats may well originate there and spill over to crop areas.

The presence of forest had generally a stronger positive effect on species richness than the presence of grasslands, while the effect on species abundance was more similar between the two semi-natural habitats (see also Taki et al. 2010). Most of the surrounding forests were composed of relatively open stands of Scots pine intermixed with broadleaf trees, and with relatively rich forest floor vegetation. The diversity of plant species and flowering phenologies in these forests is likely to provide more diverse and stable floral resources as compared to the highly disturbed intensive meadows that characterized the grassland-dominated landscapes (Klein, Steffan-Dewenter, & Tscharntke 2003; Taki, Kevan, & Ascher 2007; Watson et al. 2011). These

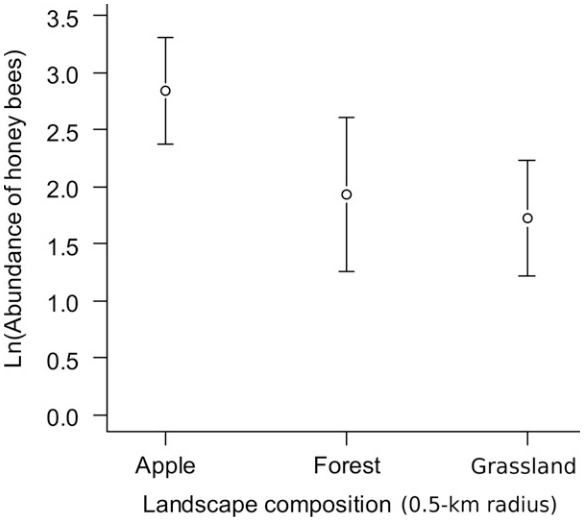

Fig. 4. Effect of landscape composition on *A. mellifera* abundance. Group means and 95% confidence intervals are presented.

meadows were highly fertilized and mown 2–4 times per year creating grass-dominated swards with low abundance of nectar-rich plants (Marini et al. 2008). The mowing further reduced the availability of the few floral resources present due to the frequent vegetation removal. Forest landscapes can be more species rich also because the flowering period of most of the forest plant species coincides with apple bloom, while grassland plant species usually bloom later in the season. It is also possible that the forested landscapes were also more heterogeneous with intermixed habitats than the landscapes dominated by intensive grasslands, thereby providing richer niche diversity. Although bee species number was higher in the forest landscapes, the two most abundant non-*Apis* species (i.e. *L. morio* and *Andrena dorsata*) were found at higher densities in the grassland- rather than in the forest-dominated landscapes indicating that even these intensive hay meadows provide suitable nesting sites and forage resources, at least for the most common bee species.

In accordance to our expectations we found that increasing elevation was associated with decreasing diversity and abundance of wild bee species. In several alpine regions, apple production is currently expanding upwards in areas formerly cultivated as hay meadows. The additive effect of simplified landscape and cold temperatures have probably created unsuitable conditions for most of the wild pollinators potentially visiting the orchards in spring. As the honey bee is generally more sensitive to cold temperatures than most of the wild species, the harshness of the climate at high elevations may pose apple orchards at higher risk of being pollinator-limited due to lower occurrence of wild species and lower activity of the honey bee. This elevation effect was, however, not strong and it differed depending on the species group considered. We found a temperature effect only for halictid and mason bees while andrenid and bumble bees were not affected. At least for bumble bees, a possible explanation for the lack of elevation effect is that these large bodied species have greater capacity to exploit cold environments due to their greater thermal inertia (Peters 1983).

Our study shows that the landscape intensification through the expansion of IPM apple monoculture drastically reduced species richness and abundance of wild bees that may potentially visit the orchards in spring. In the most extreme of these monoculture landscapes pollinator communities were almost exclusively composed of managed honey bees. The dependence on a single pollinator species is particularly risky because it leaves crop pollination vulnerable to the effects of parasites and diseases of that species. In the high elevation orchards, this effect was exacerbated probably by the cold temperatures suggesting a potentially higher vulnerability of the upper zone of apple crop production to pollinator limitation. Although we have demonstrated that the presence of grassland and forest enhanced species diversity and abundance of native pollinators in the orchards, more research is needed to understand how much of this bee diversity is actually providing the pollination service to the crop.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.09.003.

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