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LANDSCAPE FEATURES ARE A BETTER CORRELATE OF WILD PLANT POLLINATION THAN AGRICULTURAL PRACTICES IN AN INTENSIVE CROPPING SYSTEM

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Abstract

Organic farming is commonly associated with increased pollinator diversity and abundance, but the net effects on pollination rates are less documented. Besides, organic farms are often surrounded by more diverse landscapes than conventional farms, such that the contributions of landscape diversity vs. farming practices to pollination rates are often confounded with each other. Here, the roles of local vs. landscape scale variables on pollination rates of experimental plants are examined in agricultural landscapes. To this end, fruit set and seed production were measured in the obligate insect-pollinated *Lotus corniculatus*. Plants were located in pairs of neighbouring organic vs. conventional farms, which were characterized by contrasting landscape structures and compositions. Fruit set, a proxy for pollinator visitation rates, was significantly related to landscape variables: fruit set was higher in farms close to a patch of semi-natural habitat, but lower in landscapes with a high cover of semi-natural habitats. Fruit set also correlated with local variables, such as habitat type, but not with farming type. Identical pollination rates in conventional and organic farms are likely due to similar diversities of habitats, crops and weeds in both farming types of the study area. These results therefore confirm that habitat diversity prevails over pesticide-free practices to explain the higher pollinator abundances usually observed in organic vs. conventional farms.

Keywords: *Lotus corniculatus* L.; fruit set; bumblebees; organic farming; semi-natural habitats

Highlights

- The effects of farming type vs. landscape on wild plant pollination were studied
- Pollination correlated with local habitat and presence of semi-natural habitats
- In contrast, pollination rates were similar in organic vs. conventional farms
- Habitat quality appears as the main factor enhancing pollination in organic farms

1. Introduction

The ongoing loss of biodiversity in agricultural landscapes (e.g. Robinson and Sutherland, 2002) is believed to alter animal pollination, an ecosystem service essential for food production (Deguines et al., 2014; Klein et al., 2007) and for the sexual reproduction of many wild plants (Kearns et al., 1998; Ollerton et al., 2011). Beyond the simple effect of reduced numbers of pollinators, the pollination crisis may also be related to declines in the functional diversity of pollination networks, which can lower reproductive success and community persistence (Fontaine et al., 2006). Pollinator declines have been reported numerous times (Potts et al., 2010 for reviews; Steffan-Dewenter et al., 2005; Winfree et al., 2009), particularly in intensive agricultural landscapes, and the expected parallel declines of insect-pollinated plants are already observed at large scales in Europe (Biesmeijer et al., 2006). Plants provide food and habitats for many animal species involved in biological control for example, so that pollinator-induced changes in plant communities and their diversity could also have cascading effects on other ecosystem services (Scherber et al., 2010).

The design of efficient conservation schemes to reverse the loss of pollinators and pollination services in agroecosystems requires a complete understanding of the mechanisms responsible for this downward trend. Positive effects of organic farming on pollinator species richness and abundance have been documented numerous times (Clough et al., 2007; Holzschuh et al., 2010, 2008, 2007; Kennedy et al., 2013; Kremen et al., 2002; Rundlöf et al., 2008a, 2008b; Rundlöf and Smith, 2006), which suggests that agricultural practices in conventional fields are partly responsible for pollinator loss. Pesticide-free practices, together with abundant and diverse floral resources, likely provide higher quality crop and non-crop habitats and food sources in organic vs. conventional farms. Organic farms could therefore sometimes sustain populations of wild pollinators without requiring semi-natural habitats, thanks to high-quality foraging and nesting sites (Williams and Kremen, 2007).

However, the effective impact of organic farming on pollinators and pollination is still open to discussion. First, the actual effects of organic farming often depend on the landscape context, with higher benefits in intensive landscapes (Holzschuh et al., 2007; Rundlöf and Smith, 2006). Second, organic farms often encompass a larger proportion of semi-natural habitats (e.g. grassland, field boundaries or hedgerows) than conventional farms (Feber et al., 2007; Fuller et al., 2005; Gibson et al., 2007; Norton et al., 2009). Pollinator abundance and diversity are known to depend on the presence and proximity of semi-natural habitats (reviewed in Ricketts et al., 2008), which provide both nesting sites and foraging resources, so that the observed positive effects of organic farming on pollinators could be mostly attributable to a landscape effect, which has considerable implications to design conservation schemes. Finally, most studies of the impact of agricultural practices have focused on pollinator diversity and abundance (Andersson et al., 2012; but see e.g. Brittain et al., 2010b; Carvalheiro et al., 2010), whereas pollinator abundance and pollination efficiency are sometimes only weakly correlated (Ricketts et al., 2008). There is thus a need to (1) further disentangle the relative effects of in-field agricultural practices (influencing the quality of the agricultural matrix as a foraging and nesting resource) vs. landscape features (isolation from semi-natural habitat) on pollination, and (2) measure actual pollination efficiency as a necessary complement to pollinator abundance.

Here, the pollination rate of potted birdsfoot trefoil plants (*Lotus corniculatus* L., Fabaceae), estimated in terms of fruit and seed set, was compared across contrasting landscapes using a paired design (eight pairs of organic/conventional farms) in an intensive agricultural region in France. The following questions were specifically addressed: (1) Is wild plant pollination higher in organic vs. conventional farms regardless of landscape features? If organic practices favour pollinator survival and reproduction in the agricultural matrix, a positive effect of organic farming is expected irrespective of the distance to or proportion of semi-natural habitats in the surroundings. (2) How do semi-natural habitats influence pollination rates in farms? An increase in pollination rates is expected closer to semi-natural habitats (if the latter act as sources of pollinators) or with larger proportions of semi-natural habitats (as providers of food resources), at least in conventional farms.

2. Material and methods

The pollination of experimental plants was monitored in eight pairs of crop farms in the intensive agricultural region surrounding Paris, France. Each pair consisted of one conventional and one organic farm located close to each other (supplementary Fig. 1, mean distance between paired farms 2915 m; range: 490-6000 m). A farm is defined as a collection of fields managed by the same person, hence under identical practices. Organic farms are rare in the study region, such that their fields are often interspersed with conventional fields. To avoid confounding effects of neighbouring agricultural practices (e.g. contamination by pesticides from an adjacent conventional field) eight organic farms consisting of clustered fields were sampled first. A conventional farm of similar size was then selected within five km of each organic farm (supplementary Fig. 1). The eight pairs of farms were located in contrasting landscapes, which were described a posteriori by the quantity and proximity of semi-natural habitats (see section 2.2).

All farms grew mainly cereals, the dominant crops in the study region, except one organic farm that also included a few grasslands and a small sheep herd. Organic farms grew a significantly larger number of crops than conventional farms (Supplementary Table 1; mean ± SD: 9 ± 2.4 in organic farms vs. 5.6 ± 1.1 in conventional farms, Student’s test, $P = 0.005$). Some of the supernumerary crops grown in organic farms are pollinator-attractive plants, so that one may expect higher pollinator visitation rates in organic farms. Note however that pollinator-attractive crops represented a small proportion of arable land in both farming system, and that conventional farms also grew pollinator-attractive crops (e.g. oilseed rape, Supplementary Table 1).

In each farm two experimental sites were selected in each of two habitats: set-asides and margins of cereal fields. One conventional farm (C6) contained no set-aside that year; all sites were thus located in margins of cereal fields. Set-asides contain numerous pollinator-attractive flowers in contrast to margins of cereal fields; the two habitats can be compared to evaluate the influence of local resource availability on pollination rates. Within a farm, experimental sites were chosen so that they were widely distributed over the farm area, yet never adjacent to a conventional field in organic farms (and vice versa) or to mass-flowering crops such as oilseed rape or buckwheat. No managed honeybee hive was present within the studied farms. The mean distance between two sites within a farm was 750 m (range: 175-2040 m).

2.1. *Measurement of pollination efficiency*

The self-compatible, strictly entomogamous (Ollerton and Lack, 1998) birdsfoot trefoil was used to quantify pollination by several *Bombus* species, which are abundant in the study area. The cultivated forage crop varieties Leo and Baco were chosen to minimize individual variation in morphological traits such as number of flowers per inflorescence. Wild *L. corniculatus* is common in the study region (although it was not found in the direct vicinity of the experimental sites, see below) but was not cultivated as a crop in the study area.

All plants were first grown together in an insect-proof greenhouse from April to June 2009. A total of 256 pots, each containing three to five individuals of either variety (Leo, 128 pots; Baco; 128 pots) were used for this experiment. Just before flowering, potted plants were moved to experimental sites, with four individual pots per site (two pots of each variety to prevent potential self-incompatibility among individuals of the same variety). No native *L. corniculatus* plants were found in the close vicinity of the sites. After two weeks in the field, i.e. just before farmers started harvesting fields and mowing set-asides, plants were brought back to the insect-free greenhouse. Every inflorescence was labelled and the number of flowers counted. At pod maturity, fruits of each inflorescence were counted, harvested and opened to count seeds.

A substantial number of plants were lost in the field, due either to water deprivation or to the destruction of pots by farmers or wild boars: only 93 pots from 51 (instead of 64) sites were retrieved. This loss created two imbalances in the dataset: there were many more pots of the Baco than of the Leo variety (78 vs. 15) and data were available for one habitat only in two farms (C5 and C8, see Supplementary Fig. 1), in addition to farm C6. However, discarding the Leo variety or the farm pairs 5, 6 and 8 did not modify our main results. Results presented here are therefore based on the full dataset.

During the experiment, positive and negative controls were grown outside and inside the greenhouse. The negative controls consisted of 12 pots of each variety kept in the insect-free greenhouse during the flowering period. Inflorescences were labelled and flowers counted (total: 694 flowers on 200 inflorescences). At the end of the experiment, no fruit was found on any of the marked branches. The positive controls consisted of three sites of four pots (two of each variety, as in the farms) located in a grassland nearby the greenhouse, surrounded by natural habitats. In the positive controls, the number of fruits and seeds per fruit was counted on each inflorescence. The between-variety difference in fruit and seed production was tested using generalized linear mixed-effects models (glmer, R package lme4), with the number of fruits or seeds as response variables and with a Poisson error and log-link function. The models included ‘Site’, ‘Pot’ (and ‘Inflorescence’ for seed production) as random factors, and ‘Variety’ as a fixed factor.

2.2. *Landscape metrics*

We used digital land-use maps (Mode d’Occupation des Sols, Institute for Planning and Development of the Île-de-France Region 2003, http://www.iaurif.org) and ArcGIS 9.2 software (ESRI 2006, Redlands) to identify artificial (arable land, other non-grassland agricultural land, built area and open urban area) vs. semi-natural habitats (woodland, perennial grassland, water bodies and non-agricultural rural land). The distance to the nearest patch of semi-natural habitat (range: 1-698 m) and the proportion of semi-natural habitat in circular buffers around each study point (250 m, 500 m, 750 m and 1000 m radius, range: 0-56 % of semi-natural habitat) were calculated for each experimental site with the Patch Analyst extension. Within farm pairs, there was no significant difference in landscape features (distance to semi-natural habitat and proportion of semi-natural habitats) between organic and conventional farms (linear models with ‘Farming type’ and ‘Habitat’ as fixed factors, $P > 0.2$).

2.3. *Statistical analyses*

We first selected the most relevant landscape scale to study the relationship between pollination and proportion of semi-natural habitats around the sites following the approach of Holzschuh et al. (2008). To this end, single-factor generalized linear mixed-effect models (glmer, R package lme4) were used to model two response variables: (1) fruit set, the proportion of flowers setting fruits on an inflorescence, with a binomial error and a logit-link function and (2) seed set, the number of seeds per fruit, with a Poisson error and log-link function. Both types of models contained ‘Pot’, ‘Site’ and ‘Farm pair’ as nested random factors; an ‘Inflorescence’ random factor was also included in the model for seed set. In this preliminary approach, the only fixed factor was ‘Proportion of semi-natural habitats’. The four buffer radii (250, 500, 750 and 1000 m) were analysed separately. The scale maximizing the variance calculated from the fixed effect component was retained: 250 m for fruit set and 500 m for seed set.

The relationship between pollination and environmental variables was examined using the generalized linear mixed-effects models above, with the same random factors but more fixed factors. The models included the following main fixed effects: Farming system (organic vs. conventional), Local habitat (field margin vs. set-aside), Distance to the nearest semi-natural habitat, and Proportion of semi-natural habitats. A number of fixed-effect covariates potentially influencing pollination or seed production were added: *L. corniculatus* variety (Baco vs. Leo), Number of flowers per pot at harvesting (as a measure of pollinator attraction of a site), and Number of *L. corniculatus* varieties per site (which was 1 when both pots of a variety were destroyed in a site). The latter variable was used as a conservative estimate of availability of compatible pollen. For fruit set, the model also included an interaction between flower number and variety number. Two-way interactions between farming system and landscape metrics, as well as between farming system and local habitat, were never significant and were omitted without affecting the outcomes of the models. For both models marginal and conditional R^2, the percentage of variance explained by fixed factors alone or by fixed and random factors, respectively, were calculated using the formulae of Nakagawa and Schielzeth (2013) for generalized linear mixed-effects models.

3. Results

The negative controls grown in an insect-proof greenhouse confirmed that seed production in *L. corniculatus* requires visitation by pollinators: none of the 694 flowers examined set fruit. In the positive controls with open pollination, the number of fruits per inflorescence and per pot differed between varieties (mean ± SD: 2.9 ± 1 fruits per inflorescence in Leo vs. 1.9 ± 1 in Baco; 20 ± 19 fruits per pot in Leo vs. 11 ± 8 in Baco), but the number of seeds per fruit was similar (8.3 ± 4 in Leo vs. 8.6 ± 4 in Baco).

Plants grown two weeks in field sites exhibited smaller fruit sets (0.7 ± 1 fruits per inflorescence; 3.4 ± 6 fruits per pot) than positive controls, with no difference between varieties (Table 1). Fruit set correlated with some local field site characteristics: it was significantly higher in set-asides than in field margins and in sites where both *L. corniculatus* varieties remained until the end of the experiment than in sites where the two pots of a given variety were destroyed (Table 1). Overall, fruit set was not related with the total number of *L. corniculatus* flowers per sites, but there was a significant interaction between number of flowers and number of varieties (Table 1): fruit set was positively related to the number of flowers in sites with a single variety, but was unrelated to flower number in sites with two varieties. There was no difference in fruit set between organic and conventional farming, regardless of local habitat type and surrounding landscape (no significant interactions between farming system and local habitat type or landscape variables). Finally, fruit set was partly predicted by landscape variables (Table 1): it decreased with increasing the proportion of semi-natural habitats surrounding the sites and with increasing isolation from semi-natural habitats (Fig. 1).

In the fields, the number of seeds per fruit was comparable to that of the positive controls (8.5 ± 6 seeds per fruit) and was explained by none of the local or landscape-scale fixed factors (Table 1). Most variation occurred at a very fine scale, i.e. among inflorescences within a pot (conditional R^2, $R^2_{\mathrm{GLMM}(c)} \approx 67\%$, most of which is explained by variance among inflorescences, Table 1). Note that this fine scale variation also explained an appreciable fraction of variance in fruit set (large among-pots variance, Table 1).

4. Discussion

This study aimed to separate the relative effects of local farming practices (organic vs. conventional farming; field margin vs. set-aside habitat) and landscape (distance to and proportion of semi-natural habitat) on pollination provided to wild plants in agricultural areas. The comparison of pairs of farms located in the same landscape showed a combination of local and landscape-scale effects, but no detectable effect of organic vs. conventional farming, on the fruit set of *L. corniculatus*. The number of seeds per fruit was unrelated to any environmental variable.

In our experiment, fruit and seed set were used as proxys for pollination efficiency. Although no data on pollinator abundance and visitation rates were available (in contrast to Brittain et al., 2010b), part of variation in fruit set can be interpreted in terms of pollinator visitation rates. Bearing in mind that pollinator visitation is required for fertilization in *L. corniculatus* (no self-fertilization, as confirmed by the caged control plants setting no fruits, see also Ollerton and Lack, 1998) and that no wild conspecifics were found in the study area, differences in fruit set should only be caused by one of the following: (1) differences in pollinator visitation rates; (2) differences in heterospecific pollen loads on pollinators, which, when large, may dilute small amounts of *L. corniculatus* pollen and impede pollen transfer (Ashman and Arceo-Gomez, 2013); and (3) differences in the availability of compatible *L. corniculatus* pollen within sites. We observed the latter effect, i.e. a negative relationship between fruit set and compatible pollen availability, as estimated conservatively by the number of *L. corniculatus* varieties remaining in a site (Table 1). However, the number of varieties per site was unrelated to other environmental variables and should not be responsible for the relationship of the latter with fruit set. Below we therefore discuss how environmental variables influence pollinator visitation and, to a lesser extent, pollen loads across spatial scales.

4.1. *Local and landscape scale effects on fruit set*

Apart from the effect of the number of varieties per site, variation in fruit set was mostly explained by local variables related to availability of floral resources and by landscape variables; both effects can be interpreted in terms of pollinator attraction and abundance. At the local scale, fruit set was higher in the more flower-rich set-asides than in field margins and in sites with more *L. corniculatus* flowers (although the latter relationship was significant only in sites with a single *L. corniculatus* variety), regardless of farming system. In other words, sites with more floral resources (either *L. corniculatus* or other weed species) were more attractive to pollinators and received more visits, which is consistent with the well-known positive effects of floral resource availability on pollinator visitation rate and behaviour (Kunin, 1997).

At the landscape scale, fruit set decreased with increasing the distance to semi-natural habitats, which again is a well-documented pattern (see Ricketts et al., 2008 for a meta-analysis) that may be explained by higher visitation rates in the vicinity of semi-natural habitats. Pollinator abundance and richness are known to depend on the proximity of semi-natural habitats, which provide nesting sites for many pollinator species (Farwig et al., 2009; Ockinger and Smith, 2007), although the consequences on seed set are often weaker (Farwig et al., 2009; Kohler et al., 2008; Steffan-Dewenter and Tscharntke, 1999), especially with flowering crop pollination (Ricketts et al., 2008).

More surprisingly, the proportion of semi-natural habitats and fruit set were negatively related, which contradicted the general expectation that semi-natural habitats, as a source of pollinators, would increase pollination service (Kremen et al., 2004). This counterintuitive pattern was however already observed elsewhere (Brittain et al., 2010b; Winfree et al., 2007) and could be attributable to several phenomena. The explanation put forward by Winfree et al. (2007), that semi-natural habitats may be of lower quality than agricultural habitats in terms of pollinator nesting sites and food sources, can immediately be dismissed here. Winfree et al. (2007) observed lower bee abundance in forest vs. agricultural or urban areas, which created a negative relationship between pollinator diversity or abundance and forest cover in the surrounding landscape. In the present study, pollination was generally higher next to semi-natural habitats (Fig. 1), which consisted in a combination of forests and grassland; these habitats are therefore unlikely to be of lower quality than intensively managed farmland.

Alternatively, semi-natural habitats may offer abundant foraging resources to pollinators; they would therefore be more attractive than agricultural areas. Small patches of plants isolated in an otherwise hostile agricultural matrix should therefore receive few visits if abundant resources are available in the surrounding semi-natural habitats (Dauber et al., 2010; Wilcock and Neiland, 2002). The attractive effects of semi-natural habitats should depend strongly on pollinator foraging distance (Wilcock and Neiland, 2002). Bumblebees, the main pollinators of *L. corniculatus*, are large insects with potentially long foraging distances, but they depend on the presence of nearby foraging resources (optimal foraging theory). Their foraging distance can thus become short (less than 300 m, the buffer radius in our study) if floral resources are available in the nest vicinity (Wolf and Moritz, 2008), so that they may prefer foraging in nearby flower-rich semi-natural habitats than in the flower-poor agricultural matrix. In addition, the diversity of floral resources associated with more abundant semi-natural habitats may increase pollen limitation via the deposition of heterospecific pollen (Wilcock and Neiland, 2002).

4.2. *Organic farming is not associated with increased fruit set*

The absence of a relationship between fruit or seed production in *L. corniculatus* and farming system may appear at odds with numerous previous observations of higher pollinator richness and abundance, and sometimes seed or fruit production, in organic vs. conventional farms (Andersson et al., 2012; Bengtsson et al., 2005 for a meta-analysis; Holzschuh et al., 2008; Kennedy et al., 2013). However, in these studies, organic farms sometimes differed in many respects from conventional farms, including field management (use of synthetic inputs), farm-scale diversity (number of crops, presence of non-crop vegetation) and landscape configuration or composition, all of which can influence pollinator abundance and behaviour. Importantly, these studies showed that local and landscape factors can interact, such that for example the benefits of organic management should be highest in simplified landscapes (e.g. Bengtsson et al. 2005; Kennedy et al. 2013) or landscape effects should be highest as farms become increasingly simplified (Kennedy et al. 2013). The former interaction was not observed in the present study (no significant interaction between landscape variables and farming type). However, this and other studies are consistent with a predominant role of landscape variables over farming system in simplified farms, characterized by low habitat or weed diversity: Kremen et al. (2002) in Californian watermelon fields, Winfree et al. (2008) in four crops of North-Eastern USA, Brittain et al. (2010b) in Italian vine fields, or Carvalheiro et al. (2010) in South-African mango fields. In this study, farming was intensive and characterized by a low diversity of crop and non-crop habitats, even in organic farms. Although the number of crops was higher in organic than in conventional farms, cereals were the dominant crop and pollinator-attractive crops represented small proportions of cropland in both farming types. Hedgerows, field margins, and permanent set-asides were rare and weeds were controlled in both farming systems, although with different methods (e.g. set-asides were frequently mown in organic farms). As a consequence, pollinator visits were generally rare in agricultural habitats, especially in margins of cereal field: fruit set, but not seed production per fruit, was lower than that of positive controls, and lower than that of similar *L. corniculatus* pots located in urban areas (Pellissier et al., 2012).

This study therefore corroborates earlier results indicating that at a local scale, the beneficial effects of organic farming on pollinators are attributable to the diversity of habitat and food sources they provide, much more than to the absence of pesticides. For example, Holzschuh et al. (2008) showed that “species richness of flowering plants” or “flower cover” could be substituted for “farming system” in models explaining variation in pollinator abundance in fallow strips and detected no significant effect of insecticides. Similarly, Carvalheiro et al. (2011) demonstrated that the presence of weeds allowed pollinators to persist in sunflower fields, sometimes reversing the negative effects of distance to natural habitats. In the organic farms studied here, which were little diversified, exclusion of pesticides is therefore unlikely to benefit pollinators, because the latter do not use organic crops or non-crop elements much as habitats. Conversely, pesticide applications in conventional farms are likely to have limited, transient negative impacts on pollinators by affecting only a small fraction of foraging individuals (see Brittain et al., 2010a for an example of such transient decrease in pollinator visitation rates after pesticide application). Regardless of pesticide effects, the patterns observed here are consistent with the prediction of Kennedy et al. (2013) that transition to organic monocultures, with little on-farm habitat diversity, may be detrimental for pollinators.

4.3. Limitations and perspectives

Our study showing significant effect of landscape variables, but no effect of farming system, on pollination rates was restricted in space, time and pollination type. First, the dominant effect of landscape and semi-natural habitats on pollination rates may be of special significance for *L. corniculatus*, a specialist plant pollinated by a large generalist pollinator, because many other plant species may satisfy the foraging needs of bumblebees in semi-natural habitats. Contrasting patterns could be observed for plants visited by different pollinator communities (e.g. generalist plants pollinated, among others, by specialist pollinators). For example, the effects of local practices may be stronger for smaller pollinators, which usually have smaller foraging distances (Benjamin et al., 2014). Second, there was no significant effect of organic farming on pollination over a two-week period, which suggests identical pollinator visitation rates over this time frame. However, pollination rates may differ at other times (e.g. just after pesticide applications, Brittain et al. 2010a), which could result in a lower cumulative reproductive success of wild plants over the longer term. Gabriel and Tscharntke (2007) showed for example a higher proportion of insect-pollinated arable weeds in field edge and field centre of organic vs. conventional farms, suggesting such a long-term benefit of organic farming. This effect of organic farming could be mediated by the diversity of floral resources and habitats, but longer-term studies are nonetheless needed to assess plant reproductive success in both farming systems, with quantification of pollinator abundance, visitation rate and floral resources in cultivated as well as non-cultivated areas.

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FIGURE CAPTIONS

Figure 1: Relationship between *L. corniculatus* fruit set and landscape variables. Fruit set is the proportion of flowers setting fruit. Each point represents one pot (hence a maximum of 4 points per site). The two landscape variables were the proportion of semi-natural habitat in a 250-m radius buffer around a site (a) and the distance to the nearest patch of semi-natural habitat (b).

Tables

Table 1: Mixed-effects modelling of the effects of local and landscape variables on fruit and seed set of *L. corniculatus*. Stars indicate significance levels: * = 0.01 < P < 0.05; ** = 0.001 < P < 0.01; *** = P < 0.001. $R^2_{\mathrm{GLMM}(m)}$ and $R^2_{\mathrm{GLMM}(c)}$ are the marginal and conditional R-squared, i.e. the variance explained by fixed factors alone or by fixed and random factors, respectively in generalized linear mixed-effects models (Nakagawa and Schielzeth, 2013).

	Fruit set		Seed set	
Fixed factors	Estimate	[95% CI]	Estimate	[95% CI]
Intercept	-7.99	[-11.1;-4.86]	1.66	[1.08;2.25]
Farming system (conventional)	0.20	[-0.70;1.11]	0.24	[-0.079;0.55]
Local habitat type (set-aside)	**1.35****	**[0.42;2.28]**	0.23	[-0.07;0.52]
Distance to semi-natural habitats	**-0.0039***	[-7.3 10^{-2};-4.6 10^{-4}]	7.2 10^{-4}	[-1.7 10^{-3};2.5 10^{-4}]
Proportion semi-natural habitats	**-6.25****	**[-9.9;-2.6]**	-0.84	[-2.0;0.31]
Variety (Leo)	-0.25	[-1.3;0.76]	-0.11	[-0.49;0.27]
Number of flowers	0.070	[0.023;0.12]	2.2 10^{-3}	[-2.7 10^{-3};7.110^{-3}]
Number of varieties	**4.51*****	**[2.6;6.4]**	0.057	[-0.24;0.35]
Nb. flowers × Nb. varieties	**-0.039****	**[-0.069;-0.009]**		
Random factors	Variance components		Variance components	
Farm pair	0.726		<10^{-4}	
Site	<10^{-4}		<10^{-4}	
Pot	1.202		0.0693	
Inflorescence	-		0.203	
$R^2_{\mathrm{GLMM}(m)}$	38.95%		11.24%	
$R^2_{\mathrm{GLMM}(c)}$	50.76%		66.71%	

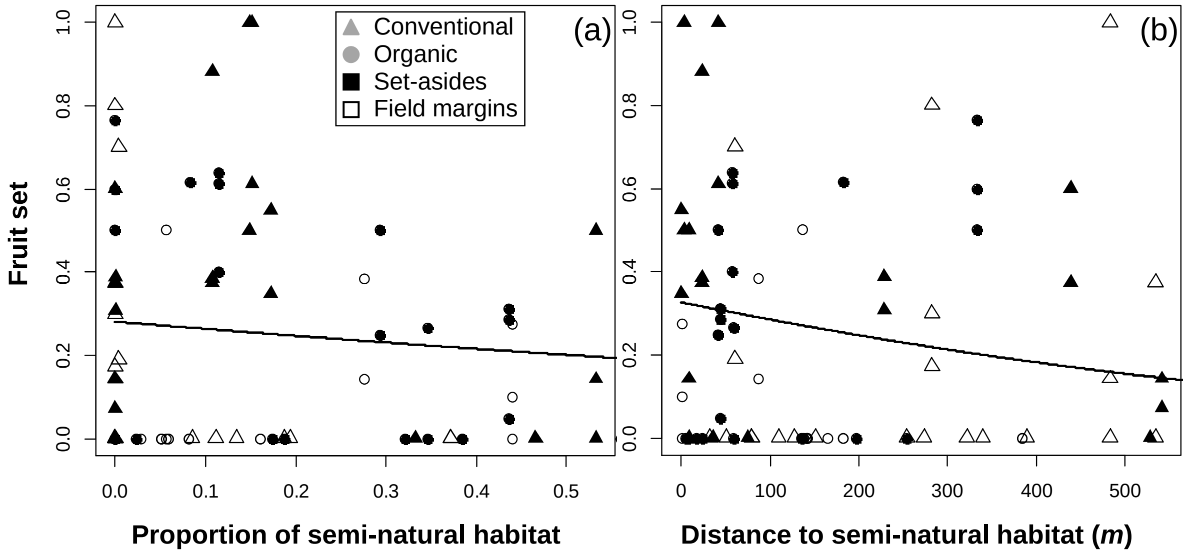
Fruit set
1.0
0.8
0.6
0.4
0.2
0.0
(a)
Conventional
Organic
Set-asides
Field margins
0.0
0.1
0.2
0.3
0.4
0.5
Proportion of semi-natural habitat
(b)
0
100
200
300
400
500
Distance to semi-natural habitat (*m*)

Figure 1