

Assessing the effect of the time since transition to organic farming on plants and butterflies

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Summary

1. Environmental changes may not always result in rapid changes in species distributions, abundances or diversity. In order to estimate the effects of, for example, land-use changes caused by agri-environment schemes (AES) on biodiversity and ecosystem services, information on the time-lag between the application of the scheme and the responses of organisms is essential.

2. We examined the effects of time since transition (TST) to organic farming on plant species richness and butterfly species richness and abundance. Surveys were conducted in cereal fields and adjacent field margins on 60 farms, 20 conventional and 40 organic, in two regions in Sweden. The organic farms were transferred from conventional management between 1 and 25 years before the survey took place. The farms were selected along a gradient of landscape complexity, indicated by the proportion of arable land, so that farms with similar TST were represented in all landscape types. Organism responses were assessed using model averaging.

3. Plant and butterfly species richness was *c.* 20% higher on organic farms and butterfly abundance was about 60% higher, compared with conventional farms. Time since transition affected butterfly abundance gradually over the 25-year period, resulting in a 100% increase. In contrast, no TST effect on plant or butterfly species richness was found, indicating that the main effect took place immediately after the transition to organic farming.

4. Increasing landscape complexity had a positive effect on butterfly species richness, but not on butterfly abundance or plant species richness. There was no indication that the speed of response to organic farming was affected by landscape complexity.

5. *Synthesis and applications.* The effect of organic farming on diversity was rapid for plant and butterfly species richness, whereas butterfly abundance increased gradually with time since transition. If time-lags in responses to AESs turn out to be common, long-term effects would need to be included in management recommendations and policy to capture the full potential of such schemes.

Key-words: agri-environment scheme, farming system, farmland biodiversity, *Lepidoptera*, time since transition

Introduction

During the last 60 years, agriculture has been characterised by rapid mechanisation and intensification (Stoate *et al.* 2001, 2009; Tilman *et al.* 2001). This has resulted in increased food production, but there have been negative consequences for the environment such as loss of biodiversity (Wilson & Aebischer

1995; Van Swaay & Warren 1999; Kleijn & Sutherland 2003) and a reduction in ecosystem services (Tilman *et al.* 2001; Kremen, Williams & Thorp 2002).

Within the European Union, agri-environment schemes (AES) have been employed as incentives to farmers to promote environmental stewardship (Kleijn & Sutherland 2003). Organic farming is encouraged under AESs because it relies on using and facilitating natural processes rather than on large external inputs. With greater variability in crop rotation and exclusion of pesticides, inorganic fertilisers and genetically modified crops, organic farming can counteract the deterioration of the agricultural landscape seen under intensive

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agriculture (Hole *et al.* 2005). The positive effects of organic farming on biodiversity have been widely reported in the scientific literature. In general, organic farming promotes biodiversity, but variable results among studies suggest that farming system *per se* may not always be the major driver of the observed species responses (Bengtsson, Ahnström & Weibull 2005; Hole *et al.* 2005).

Land-use or environmental changes typically do not lead to immediate population extinctions or colonisations but exert effects over a longer time frame (Chamberlain *et al.* 2000; Kuussaari *et al.* 2009; Jackson & Sax 2010). When a farm converts to organic farming, a positive effect on local biodiversity is expected (Rundlöf, Edlund & Smith 2010) but it might take some time before species can respond and for the potential benefits to be manifested (Younie & Armstrong 1995; Hyvönen 2007; Andersson, Rundlöf & Smith 2010). Hence, the patch (or the landscape) may be in possession of a colonisation credit, i.e. a mismatch in the number of species yet to colonise following habitat improvement and the theoretical richness based on the patch spatial properties (Cristofoli *et al.* 2010). The length of the time-lag will depend on a multitude of factors such as vegetation succession, the presence of source areas for the recolonisation of species, degradation of pesticides and nutrients, and restoration of pest/natural enemy interrelations. Here, we collectively term these factors as *effects of time since transition*.

The speed with which species respond to altered farming practice is also likely to depend on landscape context. Landscape heterogeneity (Benton, Vickery & Wilson 2003; Smith *et al.* 2010) and the presence of non-crop habitats (Marshall & Moonen 2002; Tscharntke *et al.* 2005; Öckinger & Smith 2007) have been emphasised as key factors determining biodiversity in agricultural landscapes. In landscapes where non-crop habitats are small and fragmented, a prolonged response time is expected because there will be fewer source habitat patches of sufficient size and quality, dispersal barriers such as large arable fields hampering colonisations (Jackson & Sax 2010) and a poor matrix quality (Perfecto & Vandermeer 2010).

Previous studies comparing biodiversity between farming systems have rarely incorporated or analysed temporal effects explicitly. The few long-term studies have used data from experimental farms, often in unreplicated landscapes (Mäder *et al.* 2002; Manhoudt, Visser & De Snoo 2007; Lundkvist *et al.* 2008; Taylor & Morecroft 2009). Other studies have examined the consequences of large-scale changes in agricultural landscapes. For example, Chamberlain *et al.* (2000) showed that the response of farmland birds to agricultural intensification had a time-lag of about 8–10 years over England and Wales. However, as far as we are aware, evaluations of a time since transition effect on authentic farms in replicated landscapes have only been made by Riesinger & Hyvönen (2006), studying weed species composition (but see also Kleijn & van Zuijlen 2004).

This study is the first to assess the effect of time since transition on species richness and abundance by comparing farms that have been managed organically for different periods of time in matched landscapes. We recorded the responses of two

groups of species with contrasting life histories, herbaceous plants and butterflies, to organic farming by focusing on time since transition, landscape context and their interactions. We expected higher species richness and abundance (i) on organic farms compared with conventional farms, (ii) with time since transition to organic farming and (iii) with increasing landscape heterogeneity. We also expected (iv) that species richness in response to time since transition would increase faster in heterogeneous landscapes.

Materials and methods

The study was conducted in the Provinces of Uppland and Scania, Sweden (Fig. S1 in Supporting Information). Uppland and the northernmost part of Scania mainly consist of a mixture of arable fields, pasture and forest. In contrast, the southern part of Scania, and in particular the south-west, is dominated by a homogeneous landscape with intensive agriculture. The variation in agricultural intensity was reflected in the amount of active substance of insecticide, herbicide and fungicide; in 2006, these were 3–9 times higher per treated area in Scania compared with Uppland (Statistics Sweden, 2009).

STUDY SITES

In each province, we studied 10 conventional and 20 organic farms (i.e. 60 farms in two provinces). The organic farms varied in time since transition to organic farming from 1 to 25 years. We used this approach as a substitute for real time-series data to verify possible temporal effects, as it was not possible to collect data over an equivalent period of time. All farms were selected so that they were distributed along a gradient of landscape heterogeneity, measured as the proportion of arable land (Purtauf *et al.* 2005; Roschewitz *et al.* 2005; Rundlöf & Smith 2006) within a radius of 1000 m from the sampling point. Hence, high proportional values indicate a homogeneous landscape. This approach ensured that farms differing in both farming system and time since transition would be represented in all landscape types. The landscape index was based on landscape analyses made using ArcGIS 9.3 (ESRI Inc., Redland, CA, USA) and ranged from homogeneous agricultural landscapes (proportion of arable land > 0.80) to more structurally complex landscapes with higher amounts of non-crop habitat, mainly forest (proportion of arable land < 0.25). Although forested landscapes can be relatively homogeneous in themselves, a forest-dominated matrix has been shown to benefit butterfly species richness compared with a matrix dominated by arable land (Bergman *et al.* 2008). We used data on land use in the year before the field study commenced, i.e. 2008, from The Swedish Board of Agriculture and The Swedish Mapping, Cadastral and Land Registration Authority. All organic farms were certified according to Council Regulation 834/2007 [Council Regulation (EC), 2007] and its amendments, as regulated by the European Union. The majority of the organic farms were also certified according to KRAV, the most widespread Swedish trademark for organic products, following the European regulations but with stricter rules regarding, for example, animal care. However, differences in regulations were not expected to have any implications for management overall. No consideration was given to whether farm production was crop or animal oriented.

On each farm, we established one 250-m transect in the uncultivated margin to a cereal field. Because the field margins at the farms differed in width, observations were only made up to 1.5 m from the field border, corresponding to the narrowest of the surveyed margins

in each province. In order to reduce the likelihood of local factors confounding the results, field margins adjacent to paved roads, forests, grasslands, pastures, flowering crops, watercourses or land under different farming systems were excluded. All transects were placed in field margins adjacent to ditches, minor non-paved roads and cereal fields of the same farming system. If several locations on a farm matched the criteria, selection was based on field inspection to achieve the best spread along the proportion of arable land gradient. To capture diversity within fields, two transects were also established within fields at 50 and 200 m from the beginning of the margin transect, perpendicular 50 m into the field.

SPECIES SURVEYS

Herbaceous plants

Species richness of herbaceous plants, including grasses (hereafter referred to as plants), was surveyed twice, at the end of June and July 2009. All species were recorded in 10 inventory squares, 0.3 × 0.3 m, evenly distributed in the field margin at *c.* 0.25 m from the field border. In the two within-field transects, the inventory squares were placed at 1, 5, 10, 20 and 40 m from the field border, resulting in a total of 20 inventory squares per farm. Additionally, at five occasions between May and August, species richness of plants in bloom was also recorded. However, as plant species richness was highly correlated with species richness of plants in bloom ($r = 0.84$) and because non-flowering plants are important as butterfly host plants, shelter, etc., we only included species richness as a measure of butterfly habitat quality in the analyses. Data from the field margins and within fields were pooled in the analyses. Krok & Almquist (2003) and Mossberg & Stenberg (2003) were used for species identification and nomenclature.

Butterflies

Between June and August 2009, surveys of butterflies (*Rhopalocera*) and burnet moths (*Zygaenidae*) (hereafter collectively referred to as butterflies) were carried out on five and six occasions in Uppland and Scania, respectively. Using a modified version of the widely implemented survey method 'Pollard walk' (Pollard & Yates 1993; Öckinger *et al.* 2006), all butterflies 5 m ahead, 5 m into the field and 1.5 m into the field margin were identified to species. Surveying was only carried out between 9 AM and 5 PM (Central European summer time, UTC +2) in sunny conditions at temperatures of 17 °C or over and without strong wind (≤ 4 on the Beaufort scale). At higher temperatures, some cloud cover was accepted as higher temperatures can compensate for less sun (Wikström, Milberg & Bergman 2009). To avoid bias among species' diurnal activity pattern (Wikström, Milberg & Bergman 2009), all surveys were randomly allocated during the course of the day. The taxonomy of species follows Eliasson, Ryrholm & Gärdenfors (2005).

STATISTICAL ANALYSES

We used an information theoretical approach based on Akaike's Information Criterion (AIC) (Akaike 1974) to analyse how plant species richness and butterfly species richness and abundance were related to farming system, time since transition to organic farming and landscape composition. In contrast to stepwise regression analyses, AIC is a likelihood-based measure allowing models differing in numbers of predictor variables to be compared and deflating the probability of type 1 errors (i.e. false-positive results). Also, AIC does

not always select a single best model but instead can recognise other candidate models with similar fit (Whittingham *et al.* 2006). Thus, this technique is able to handle model uncertainty.

First, we analysed the effect of farming system, irrespective of time since transition, by constructing a set of candidate general and generalised linear regression models in the statistical software R v 2.12.1 (R Development Core Team, 2010). We included the proportion of arable land, the province and all two-way interactions to account for responses mainly associated with landscape structure and large-scale farming intensity. The response variables were centred around the mean to reduce collinearity, allowing for the interpretation of main effects in the presence of interactions (Aiken & West 1991). All analyses were made on data pooled at the field level.

To assess the relative strength of support for the models, given the chosen parameters, we used AIC_c (i.e. AIC with a second-order correction for sample size) and Akaike weights (R package MuMIn; Barton, 2009). The latter can be interpreted as the probability of a model having the best fit among the whole set of candidate models. Models with $\Delta AIC_c < 2$ may be considered to have equal strength (Burnham & Anderson 2002). In our analyses, we could not find a single best model; therefore, we performed model averaging to circumvent the problem of competing models. This method takes the parameter estimates of all candidate models and calculates average estimates, where each model's contribution is proportional to its weight.

In a second set of candidate models, we analysed the temporal effect of organic farming, thus excluding the conventional farms in the analyses. For plants, we used the time since transition to organic farming, the proportion of arable land and their interaction as explanatory variables, using Poisson regression models with log-link function. No correction for overdispersion was necessary. In analyses of butterfly species richness and abundance, we also added plant species richness with its interactions as explanatory variables as we believed that the temporal effect on butterflies could be driven by the plants in part. GLMs assume linear relationships and because we could expect a nonlinear response of species richness and abundance to the time since transition, we included the quadratic term of time since transition to account for possible curvature. Butterfly abundance was log-transformed prior to analysis for proper Gaussian distribution, whereas butterfly species richness was square-root-transformed ($x + 10$) to achieve approximately normally distributed residuals, as a Poisson distribution caused problems with underdispersion. To visualise the relationships of time since transition and proportion of arable land to plant species richness and butterfly species richness abundance, respectively, linear regressions were created based on the average model parameters and, for comparison and illustration of field data, partial residual plots based on the model with lowest AIC_c .

Results

EFFECT OF FARMING SYSTEM AND LANDSCAPE COMPOSITION

We recorded 159 plant species, of which 151 were found in the field margins and 97 within the fields. Organic farms had *c.* 20% higher plant species richness compared with conventional farms (Table 1). No effect of the proportion of arable land in the surrounding landscape on plants was observed (Table 2).

Table 1. Average number \pm standard error of plant species richness and butterfly species richness and abundance on organic and conventional farms

	Farming system	
	Conventional	Organic
Plant richness	36.1 \pm 1.1	42.3 \pm 0.7
Butterfly richness	8.4 \pm 0.3	10.3 \pm 0.4
Butterfly abundance	42.4 \pm 2.7	68.0 \pm 5.5

$N_{\text{org}} = 40$, $N_{\text{conv}} = 20$.

In total, 3797 individuals belonging to 37 butterfly species were recorded. Organic farms supported both higher species richness (*c.* 20%) and abundance (*c.* 60%) (Table 1). An increasing proportion of arable land in the landscape was negatively related to species richness (Table 2), whereas no effect of landscape composition on butterfly abundance was found (Table 2).

EFFECTS OF TIME SINCE TRANSITION

Plants demonstrated huge variation with both high and low species richness irrespective of time since transition (Fig. 2a), and the explanatory power of time since transition was low (0.47) (Table 3). There was less variation among farms for butterfly species richness (Fig. 2b), and even if the 95% confidence

intervals of the estimated relationships between species richness and time since transition included zero, time since transition had a large relative importance (0.61, Table 3). Conversely, we found a linearly increasing effect of time since transition to organic farming for butterfly abundance (Table 3). This response was not, as hypothesised, faster in a heterogeneous landscape compared with a homogeneous landscape. Based on the average model parameter estimates, the number of butterfly individuals increased twofold between 1 and 25 years since farming system transition (Fig. 1). The field data illustrate the large variation in butterfly abundance between farms with some farms supporting relatively high abundance despite their short time under organic management (Fig. 2c).

Discussion

Organic farming has previously been shown to contribute to the conservation of biodiversity in agricultural landscapes, but information on how biodiversity develops with time since transition to organic farming is scarce. In this study, we used farms that had been under organic management for up to 25 years, allowing us to analyse the long-term responses to this change in land use. We found positive effects of organic farming on both plant species richness and butterfly species richness and abundance. However, an effect of time since transition to organic farming was only found for butterfly abundance,

Model average parameters	Estimate	SE	95% CI		Relative variable importance
			Lower	Upper	
<i>(a) Plant richness</i>					
Farmsys	0.165	0.049	0.067	0.263	1.00
Prop. arable	-0.001	0.057	-0.114	0.113	0.43
Region	0.029	0.043	-0.056	0.114	0.53
Farmsys \times prop. arable	0.014	0.032	-0.049	0.077	0.08
Farmsys \times region	-0.006	0.170	-0.039	0.026	0.10
Prop. arable \times region	-0.052	0.945	-0.237	0.134	0.15
Intercept	3.570	0.046	3.480	3.660	
<i>(b) Butterfly richness</i>					
Farmsys	0.224	0.084	0.056	0.392	0.97
Prop. arable	-0.505	0.178	-0.862	-0.149	0.99
Region	-0.026	0.052	-0.129	0.077	0.40
Farmsys \times prop. arable	0.030	0.090	-0.149	0.209	0.20
Farmsys \times region	0.002	0.011	-0.020	0.025	0.06
Prop. arable \times region	0.029	0.064	-0.098	0.155	0.10
Intercept	4.290	0.073	4.140	4.430	
<i>(c) Butterfly abundance</i>					
Farmsys	0.457	0.138	0.180	0.735	1.00
Prop. arable	-0.071	0.264	-0.594	0.451	0.51
Region	-0.462	0.136	-0.735	-0.189	1.00
Farmsys \times prop. arable	0.246	0.402	-0.546	1.040	0.27
Farmsys \times region	-0.006	0.046	-0.097	0.085	0.16
Prop. arable \times region	-0.006	0.028	-0.063	0.051	0.04
Intercept	3.860	0.128	3.610	4.12	

Table 2. Model average parameter estimates, standard errors (SE), 95% confidence intervals (CI) and relative variable importance demonstrating the effects of farming system and landscape composition on plant species richness and butterfly species richness and abundance. Analyses are made on data pooled at the field level from conventional and organic farms. Interactive effects are displayed as \times . Positive estimates indicate higher species richness and abundance on organic farms, in the Province of Uppland and with decreasing proportion arable land in the landscape, respectively

Farmsys, farming system (organic); prop. arable, proportion of arable land; region, Uppland and Scania, respectively.

Table 3. Model average parameter estimates, standard errors (SE), 95% confidence intervals (CI) and relative variable importance demonstrating the effects of time since transition to organic farming on plant species richness and butterfly species richness and abundance. Analyses are conducted on data pooled at the field level from organic farms. Interactive effects are displayed as \times . Positive estimates indicate higher species richness and abundance with time since transition, with increasing plant richness and with decreasing proportion arable land in the landscape, respectively

Model average parameters	Estimate	SE	95% CI		Relative variable importance
			Lower	Upper	
<i>(a) Plant richness</i>					
Prop. arable	0.017	0.057	-0.098	0.132	0.47
TST	1.01e-4	1.89e-3	-3.72e-3	3.93e-3	0.47
TST ²	-5.69e-5	3.04e-4	-6.70e-4	5.56e-4	0.47
TST \times prop. arable	-7.05e-4	1.60e-3	-3.86e-3	2.45e-3	0.05
Tst \times TST ²	-7.19e-6	1.57e-5	-3.82e-5	2.38e-5	0.05
TST ² \times prop. arable	-2.87e-5	9.08e-5	-2.10e-4	1.53e-4	0.03
Intercept	3.750	0.026	3.700	3.800	
<i>(b) Butterfly richness</i>					
Prop. arable	-0.422	0.204	-0.835	-0.010	0.93
TST	6.26e-3	7.09e-3	-7.88e-3	2.04e-2	0.61
TST ²	2.74e-4	6.04e-4	-9.33e-4	1.48e-3	0.34
Plant sp.	3.10e-4	2.57e-3	-4.89e-3	5.51e-3	0.29
TST \times plant sp.	-4.02e-5	9.48e-5	-2.28e-4	1.48e-4	0.03
TST \times prop. arable	-3.50e-3	7.60e-3	-1.86e-2	1.16e-2	0.14
TST \times TST ²	-3.46e-7	4.67e-6	-9.80e-6	9.10e-6	0.02
TST ² \times plant sp.	-4.26e-8	1.95e-6	-4.01e-6	3.93e-6	0.01
TST ² \times prop. arable	-8.99e-5	2.87e-4	-6.64e-4	4.84e-4	0.05
Prop. arable \times plant sp.	-1.54e-3	4.00e-3	-9.51e-3	6.43e-3	0.05
Intercept	4.500	0.045	4.410	4.590	
<i>(c) Butterfly abundance</i>					
Prop. arable	0.087	0.172	-0.257	0.430	0.35
TST	0.025	0.011	0.002	0.048	0.96
TST ²	-7.68e-5	6.00e-4	-1.29e-3	1.14e-3	0.31
Plant sp.	3.05e-5	3.60e-3	-7.30e-3	7.36e-3	0.28
TST \times plant sp.	1.49e-5	8.93e-5	-1.66e-4	1.95e-4	0.04
TST \times prop. arable	-1.64e-4	2.17e-3	-4.57e-3	4.24e-3	0.05
TST \times TST ²	2.99e-5	6.44e-5	9.77e-5	1.57e-4	0.09
TST ² \times plant sp.	5.26e-6	1.22e-5	-1.89e-5	2.95e-5	0.02
TST ² \times prop. arable	3.09e-5	1.09e-4	-1.88e-4	2.50e-4	0.01
Prop. arable \times plant sp.	2.70e-3	5.94e-3	-9.04e-3	1.44e-2	0.03
Intercept	4.040	0.072	3.900	4.190	

TST, time since transition; TST², squared term of TST; prop. arable, proportion of arable land; plant sp., plant species richness.

indicating a direct transition effect for plant and butterfly species richness.

In line with previous studies (Bengtsson, Ahnström & Weibull 2005; Hole *et al.* 2005; Holzschuh, Steffan-Dewenter & Tscharntke 2008; Rundlöf, Bengtsson & Smith 2008), we found higher species richness and diversity on organic farms. Organic farming affects many factors of importance for biodiversity, and exactly what is most important in our study is hard to identify. Of the many components of agricultural intensification, such as input of agrochemicals, crop homogenisation and loss of landscape elements, Geiger *et al.* (2010) showed that the use of pesticides was most likely to be detrimental to biodiversity. Hence, the clear distinction between farming systems in the use (conventional farming) and non-use (organic farming) of pesticides is a probable explanation for our result.

As plant and butterfly species richness responded positively to organic farming, but not to the time under organic management, it appears that the increase in species richness occurred immediately after the transition between farming systems and afterwards remained fairly constant. Hence, the increase in

species richness appears to be a consequence of the transition itself rather than the time under organic management. This fast response by plants is surprising, because grassland plants have been shown to have a longer time-lag to extinction following habitat fragmentation compared with butterflies (Krauss *et al.* 2010), which in general are assumed to respond rapidly to environmental changes (Thomas *et al.* 2004). The rapid and short-term response among plants was most probably due to the exclusion of herbicides on organic farms, which is the major factor determining farmland plant species richness between conventional and organic farming practices (Petersen *et al.* 2006). Exclusion of herbicides allows the sprouting of seeds that have survived in the seedbank as well as successful colonisation from surrounding populations. A further increase in species richness is likely to be constrained by several factors. Residual soil fertility (Walker *et al.* 2004), for example, hampers successful colonisation by favouring highly competitive plant species (Bakker & Berendse 1999). Also, studies have shown that biodiversity in agricultural landscapes are dependent on proximate semi-natural habitats functioning as population sources (e.g. Duelli & Obrist 2003) but that the effect

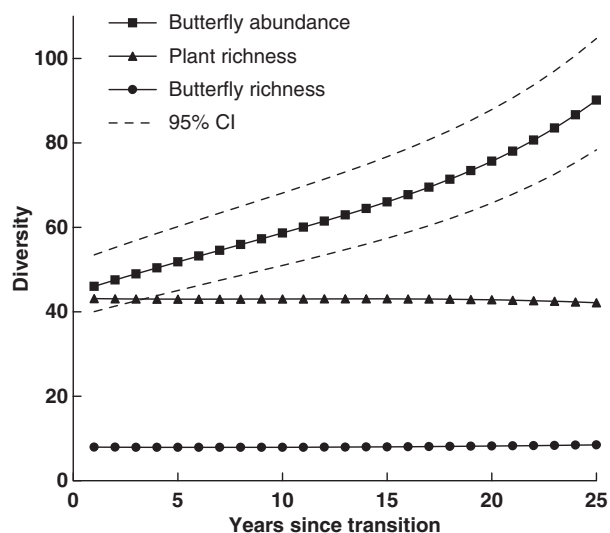


Fig. 1. Predicted plant species richness and butterfly species richness and abundance in relation to time since transition to organic farming. The figure is drawn based on model averaging parameter estimates with 95% confidence intervals.

decreases with distance to these habitats (Öckinger & Smith 2007; Kohler *et al.* 2008). A combination of little semi-natural land and intensive management on conventional farms in the surrounding landscape keeps the species pool and population sizes on a level that may not be sufficiently large enough to allow colonisation on organic farms. Rundlöf, Edlund & Smith (2010) found effects of organic farming on plants, not only on a field level but also on a landscape level. This indicates that to get the most out of organic farms in terms of biodiversity, their spatial arrangement needs to be considered. Hence, a further increase in species richness after transition to organic farming is expected to be constrained by the isolation of species and the isolation of organic farms.

In contrast to plant and butterfly species richness, butterfly abundance increased gradually with time since transition with twice as many individuals recorded after 25 years of organic management compared with that of the first year. This relatively slow response could perhaps be explained by the low carrying capacity of arable land for butterflies. The preservation and improvement of non-crop areas, such as field margins, as habitat for butterflies and other species in landscapes dominated by arable land would be valuable. Sympathetic management of field margins (Feber, Smith & Macdonald 1996) and hedgerows (Maudsley 2000) can be an effective way to enhance arthropod diversity on farmland. Furthermore, non-cropped field margins are attractive to farmers because there is minimal impact on their commercial crop and they are of low maintenance.

In this study, we found an effect of landscape type on butterfly species richness but not on butterfly abundance or plant species richness. These results are similar to those of Weibull & Östman (2003) who concluded that sedentary species (plants) are less affected by surrounding landscape features compared with mobile species (butterflies) and Öckinger *et al.* (2009)

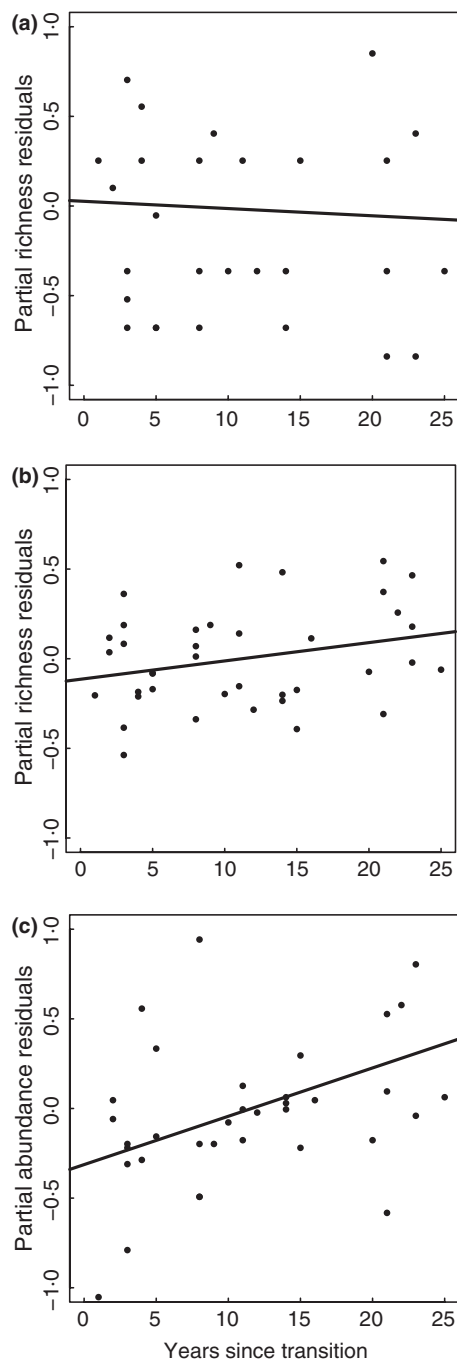


Fig. 2. Illustration of plant species richness (a) and butterfly species richness (b) and abundance (c) in relation to time since transition to organic farming. The plots show the partial residuals from the model with lowest AIC_c, and each dot represents data collected on one organic farm. AIC, Akaike's Information Criterion.

who found landscape effects for mobile but not for sedentary butterflies (see also Bengtsson 2010). It is possible that analysis of landscape effects on plants at a more local scale (< 1 km) might have given other results. However, landscape composition at the 1-km scale was correlated with composition at scales down to 300 m. Therefore, in line with Marshall (2009) and Bengtsson (2010), our results indicate that local conditions are of greater importance than the wider landscape context for

less-mobile organisms such as plants. However, the proportion of arable land is a crude measure of landscape heterogeneity that does not consider species-specific habitat requirements. In our case, we used this measure in the selection of farms as it is likely to correlate with several ambiguous aspects of landscape structure important for biodiversity (see also Purtauf *et al.* 2005; Roschewitz *et al.* 2005; Rundlöf & Smith 2006), but it may not always be the best explanation for species distributions in the landscape.

Our hypothesis that species would respond faster to local habitat improvement, such as organic farming, in heterogeneous compared with homogeneous landscapes was not supported. Such an effect was expected owing to the larger species pool in complex landscapes and the proximity to source habitats, which could facilitate colonisation of species. The lack of a landscape effect on species responses to time since transition could indicate that the gradient of landscape complexity was too narrow to detect differences in the rate of colonisation, even though we selected the most extreme cases possible under our selection criteria. It could also indicate that the species composition differed between landscape types, e.g. a dominance of highly mobile species in homogeneous landscapes. This, however, needs further study.

If the effects of AESs take a long time to be manifested, there is a risk that the schemes will not be sustained in the long term because their benefits for biodiversity and ecosystem services are not immediately obvious. Furthermore, economic validation of the costs and benefits will be difficult over longer time-scales. However, for plant and butterfly species richness, we have shown that evaluation of the effects of organic farming on biodiversity can be valid shortly after the farming system transition. By contrast, butterfly abundance increased gradually over time, indicating that a short-term approach may be risky and could underestimate the true benefits. Before any further conclusions can be drawn regarding the effect of time since transition on biodiversity, there is a need for replicate studies on several species groups. While farming system *per se* is clearly important, the underlying mechanisms behind species responses need to be identified. In particular, we need to establish what is constraining a further increase or faster response in species richness and abundance over time.

SYNTHESIS AND APPLICATIONS

It is not possible to extend our results to other organisms or landscapes without further study. However, we hypothesise that other pollinating insects with relatively high mobility may respond in a similar way to butterflies and that organisms with low dispersal ability may take a much longer time than plants or butterflies to respond to AESs or other land-use change.

If time-lags in responses to changes in land use such as AESs turn out to be common, long-term studies are imperative to properly understand and measure effects on biodiversity and ecosystem services. Assessment of such long-term effects would also need to be included in management recommendations and policy.

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Supporting Information

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Fig. S1. Map showing the location in Sweden where the study was conducted.

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