

Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale

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Summary

1. Increasing landscape complexity can enhance biodiversity and ecosystem services in agroecosystems. However, policies based on conversion of arable land into semi-natural habitats to increase landscape complexity and ecosystem services can be difficult to implement. Although it appears to be a promising management option, nothing is known about the effect of increasing landscape diversity through crop rotations on the delivery of ecosystem services.

2. In this study, we examined how landscape complexity and crop rotation intensity in the landscape at different spatial scales affect the flow and the stability of natural pest control services in barley fields using manipulative cage experiments.

3. Exclusion experiments revealed that natural enemies can have a strong impact on aphid population growth and that the delivery of pest control services is strongly dependent on the landscape context.

4. We found that the overall level of pest control increased with landscape complexity and that this effect was independent of crop rotation intensity. In addition, the within-field stability in pest control services increased with crop rotation intensity in the landscape, although stability in parasitism rates decreased.

5. Multiple spatial scales analyses showed that the mean level of natural pest control was best predicted by landscape complexity at the 0.5-km and the 1-km spatial scales. The stability in overall pest control decreased with proportion of ley at the 2.5-km and the 3-km spatial scales.

6. *Synthesis and applications.* Our study disentangled, for the first time, the relative effects of landscape complexity and crop rotation intensity on the delivery of an ecosystem service. We show that combined management of semi-natural habitat and crop rotation can stabilize and enhance natural pest control in agricultural landscapes. Our findings have important implications in terms of management options to maintain and enhance ecosystem services in agroecosystems. They suggest that conservation of heterogeneous landscapes, characterized by a higher proportion of semi-natural habitats such as pastures and relatively small fields, is essential for maintaining and enhancing effective biological control in agroecosystems.

Key-words: biological control, crop diversity, crop rotation, ecosystem services, farming practices, landscape complexity, stability

Introduction

Natural pest control provided by predators and parasitoids is an important ecosystem service supporting agricultural production (Losey & Vaughan 2006). It has been

demonstrated that natural pest control requires a landscape perspective and is influenced by several factors acting at various spatio-temporal scales, such as local crop management and landscape context (Rusch *et al.* 2010; Tscharrntke *et al.* 2007).

Among these factors, a growing body of evidence suggests that landscape complexity strongly influences natural

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enemy communities (Tschardtke *et al.* 2007). It has been demonstrated that complex landscapes with larger proportions of semi-natural habitats support more diverse and abundant communities of natural enemies (Chaplin-Kramer *et al.* 2011). However, even if the effects on natural enemies are relatively well known, very little is known about the level of natural pest control services provided by these communities and how farming practices and landscape context influence the delivery of this service (Chaplin-Kramer *et al.* 2011; Rusch *et al.* 2010).

Although there is evidence of a positive influence of semi-natural habitats on abundance and diversity of some taxa, it remains unknown whether longer and more diverse crop rotations at the landscape level, characterized by higher plant species richness and lower levels of disturbance, could be beneficial for biodiversity and associated ecosystem services (Fahrig *et al.* 2011). Crop rotation schemes at the landscape scale may affect natural enemy communities due to changes in spatial distribution of resources over time (Holland *et al.* 2005; Rusch *et al.* 2010). For instance, increasing crop diversity may be beneficial to natural enemies due to higher spatio-temporal availability of food or refuges at the landscape scale. Longer and more diverse crop rotation systems with a higher proportion of perennial crops may also reduce disturbance of natural predator communities (Jonsson *et al.* 2012), facilitating spillover of these communities into annual crops. Moreover, increasing crop diversity at the landscape scale may also alter trophic interactions by limiting pest populations' spread due to increased distances between host patches or by disrupting host location. Thus, short and monotonous crop rotations at the landscape scale, characterized by a high proportion of only a few annual species with a high level of disturbance at the field scale, may alter food web structure and reduce predator-prey interactions in ecological networks thereby limiting pest control services.

Policies based on conversion of productive arable land into semi-natural land are difficult to implement because of the economic impact on farmers and the societal need for food production (Balmford, Green & Phalan 2012). Thus, increasing within-landscape diversity by modifying crop rotations may be a promising tool for enhancing ecosystem services in agricultural landscapes that support high and stable crop yields (Bommarco, Kleijn & Potts 2012). However, because landscape variables are usually highly correlated, it is difficult to assess their individual effects on biodiversity and ecosystem services. For instance, Persson *et al.* (2010) found scale-dependent relationships between agricultural intensity and landscape complexity. Disentangling the respective effect of landscape complexity and crop rotation intensity on biodiversity and ecosystem services is thus of major importance if we are to develop efficient agro-environmental schemes (Fahrig *et al.* 2011; Jonsson *et al.* 2012).

Assessments of natural pest control delivered by entire natural enemy communities in a landscape perspective are

rare (Chaplin-Kramer *et al.* 2011). Most previous studies focus on predation or parasitism rates from a limited number of taxa and therefore do not take into account the effects of interactions between species on natural pest control (but see Gardiner *et al.* 2009). There are several relationships between natural enemy diversity and the level of pest control that have been found in terrestrial ecosystems. Different studies have reported positive, negative or neutral effects of natural enemy species richness on herbivore mortality (Letourneau *et al.* 2009). Thus, quantifying the level of pest control by the entire natural enemy community according to landscape context is of considerable importance if we are to design functional agricultural landscapes. Moreover, understanding the stability of ecosystem services through time and space is of particular importance in this context as it contributes to reliable crop productivity (Bommarco, Kleijn & Potts 2012). It has been shown that beta diversity increases with landscape complexity and decreases with agricultural intensification (Karp *et al.* 2012; Tschardtke *et al.* 2007). Thus, complex and/or less intensively cultivated landscapes are assumed to support more resilient communities and more stable ecosystem services through time and space due to higher diversity per functional group. However, the spatio-temporal variability of natural pest control in relation to landscape characteristics and farming practices remains largely unexplored.

The spatial scales at which natural enemies respond to landscape complexity vary depending on species functional traits such as trophic level or body size (Tschardtke *et al.* 2007). While several studies have explored how particular species or taxa respond to different spatial scales, the scale-dependency of overall biological control efficacy (i.e. the magnitude of pest suppression due to all natural enemies and resulting from any interactions among natural enemies) is poorly studied.

In this study, we combined a 'mensurative experiment' with experimental manipulation (Scherber *et al.* 2012) to examine the relative effects of landscape complexity and crop rotation intensity on the level and the stability of biological control of cereal aphids in southern Sweden. Using a design in which complexity and crop rotation intensity in the landscape were orthogonal factors, we were able to disentangle the relative effects of these variables on pest control services. We hypothesized that the level and the stability of pest control services would increase with landscape complexity and with the proportion of crop rotation schemes that include both perennial and annual crops in the landscape (low crop rotation intensity). We also hypothesized to find an additive or synergistic effect of landscape complexity and crop rotation schemes on the level of natural pest control as a result of complementarity between semi-natural and arable land components at the landscape scale. We predicted that natural pest control should be maximized in complex landscapes supporting more extensive crop rotations.

Materials and methods

STUDY DESIGN AND LANDSCAPE ANALYSIS

We established a study system in the province of Skåne in southern Sweden that allowed testing for the respective effects of semi-natural habitats and crop rotation intensity at the landscape scale on natural pest control services. Our study system consisted of 19 conventional spring barley fields selected along two orthogonal gradients: a gradient of proportion of ley in the landscape and a gradient of landscape complexity.

The proportion of ley in the landscape was used as a proxy for crop rotation intensity and crop diversity at the landscape scale. Leys are composed of perennial crops such as grass and clover that are cultivated for forage production and are less intensively managed than annual crops. In Skåne, typical crop sequences that include ley are a 6-year crop sequence (barley undersown with clover and grass/ley/ley/winter oilseed rape/winter wheat/oats or barley) and are longer, less disturbed and more diversified than the classic crop sequence (barley/winter oilseed rape/winter wheat/winter wheat). Thus, landscapes with large average proportions of ley support fields with longer and more diversified crop rotations than landscapes with low average proportions of ley.

Landscape complexity can be measured by various metrics. On the basis of the results of Persson *et al.* (2010), we used a proxy for landscape complexity based on the amount of pasture (square root-transformed) and the length of field borders in the landscape. Following Persson *et al.* (2010), these two variables were combined into one variable using principal component analysis (PCA). The first axis of the PCA was then used as a measure of landscape complexity for field selection and data analysis. We used values from the first axis of the PCA (PC1) based on landscape variables calculated from non-overlapping 1-km radius landscapes covering most (80%) of the main agricultural areas of Skåne for farm selection. To ensure that landscapes varied more along PC1 than PC2, all landscapes that had a standard deviation greater than one along the PC2 axis were excluded. Larger values on the first PCA axis represented more heterogeneous landscapes, with more pastures and more field borders, and lower values represented more homogeneous landscapes, with less pastures and fewer field borders. PC1 values at 1 km spatial scale ranged from -1.38 to 2.11 . Note that pastures and leys are relatively different habitats. Leys are rotational crops cultivated for grazing, hay or silage production, whereas pastures are practically permanent, semi-natural grasslands exclusively used for grazing and generally not fertilized.

Information on land-use characteristics was available from the Integrated Administration and Control System (IACS), a data base developed by the Swedish Board of Agriculture. This spatial data base was used in ArcGIS (ESRI Inc., Redland, CA) to select farms and landscapes and to calculate the land-use statistics.

Sites were selected by a two-step procedure: (i) farm selection and (ii) field selection within farms. For farm selection, we computed the average proportion of ley in the landscape between 2009 and 2011 and the first PCA axis using the IACS data for any potential independent landscapes in the study region (i.e. non-overlapping landscapes). The scale used for sites selection was 1 km. To ensure that landscape complexity and proportion of ley in the landscape were orthogonal, we selected landscapes with as equal representation as possible of average proportion of

leys (low, intermediate and high) along the landscape complexity gradient. On each selected farm, we then selected the barley field closest to the centre of the landscape. The first PCA axis and the average proportion of ley between 2009 and 2011 in the landscape around the selected field were recomputed for the selected field to validate our selection procedure. The landscape characteristics around the selected fields and the landscape characteristic used for farm selection were highly correlated (correlation = 0.99). This procedure makes it possible to build a design with two orthogonal factors (i.e. landscape complexity and crop rotation intensity) (see Table S1 in Supporting Information). These landscape variables were then computed at six spatial scales from 0.5 km to 3 km radii (0.5-km intervals) around fields (centre of the experimental plot) and used as explanatory variables. Inevitably, landscape variables were less orthogonal at larger spatial scales. However, collinearity among predictors was examined, and there were no collinearity problems for any model at any scale (see data analysis).

EXPERIMENTAL DESIGN AND BIOLOGICAL CONTROL ASSESSMENT

At each selected site, the experiment was set up in a 20×100 m strip located at the edge of the field. No pesticides were used in the experimental area, and the experiment took place during the milk ripening stage of the crop. The experimental design consisted of four replicates each of two natural enemy treatments located along a transect in the middle of the strip. The two natural enemy treatments were as follows: (i) a cage treatment, where all epigeal and flying natural enemies were excluded and (ii) an 'open' treatment, where all natural enemies had access to the plants. For each pair, cage and open treatment were randomly allocated along the transect and separated by 2 m. Pairs were separated by 5 m. Cages were cylindrical and made of solid plastic fine mesh (mesh size: 0.5 cm; diameter: 0.3 m, height: 1 m). The cages were inserted in a metal ring 0.3 m in diameter and 0.25 m in height. The metal ring was dug 10 cm into the soil, and the plastic cages were covered with a sticky glue to ensure that no natural enemies could enter the cage (Thies *et al.* 2011). In all cages, natural enemies were actively searched out and removed by hand, and a pitfall trap filled with a water-detergent mix was added to ensure that no natural enemies remained within the cage.

For each replicate of each treatment, one pot containing eight barley plants (Cv.: Scandium) previously infested with three late instar bird cherry-oat aphids *Rhopalosiphum padi* per plant (24 aphids per pot) in the laboratory was carefully placed in the field to soil level. Aphids used in the experiments were unwinged individuals obtained from a laboratory colony maintained on barley. The time between aphid inoculation and placement in the field was 5 days, allowing time for aphid reproduction. Numbers of aphids per pot were recounted just before placement into the field, and replicate pots were paired according to the actual number of aphids to ensure similar abundance between treatments. Due to reproduction and disturbance during transportation, the number of aphids per pot was different compared with the initial number of aphids inoculated. However, using a paired design makes it possible to assess the cage effect and estimate the mortality due to natural enemies.

Pots were collected after 5 days, and the number of aphids per pot was recounted. For each field, suppression of aphids due to

natural enemies was quantified as the average proportion of aphids predated in the open treatment compared with aphid populations in the cage treatment, following:

$$\text{Biological control} = \frac{\sum_{i=1}^4 \left(1 - \frac{A_{\text{open } 5i}}{r_{\text{cage}_i} A_{\text{open } 0i}} \right)}{n}$$

where $A_{\text{open } 5i}$ is the number of aphids in the open treatment after five days, $r_{\text{cage } i}$ is the aphid population growth in the cage treatment calculated as the ratio of final to initial aphid numbers, $A_{\text{open } 0i}$ is the number of aphids in the open treatment at the beginning of the experiment, i is the replicate number and n is the number of replicates for a given field. This metric ranges from 0 to 1, where 0 indicates no net loss of aphids in the open treatment and 1 indicates that 100% of aphids was predated. The estimate of aphid suppression due to natural enemies was found to be negative in 6 cases of 76 because there were more aphids in the open treatment than in the cage treatment. Following Gardiner *et al.* (2009), a biological control value of zero was assigned to these cases as this indicates no effective biological control.

All parasitoid mummies found on the open treatment plants were counted and individually collected at the end of the experiment. For each replicate, the open treatment pots were kept individually in a glasshouse for 3 weeks after the end of the experiment and mummies were regularly collected. Collected mummies were reared in the laboratory for identification, and parasitism rates were calculated as the ratio between the number of mummies and the total number of aphids at the end of the experiment in the cage treatment.

To assess the within-field variability in biological control, we calculated the coefficient of variation (the standard deviation relative to the mean) in overall biological control and in parasitism rates for each field.

DATA ANALYSIS

Linear mixed-effect models were used to analyse the effects of the cage treatment on the average aphid populations at the beginning and at the end of the experiment. The fixed factor was the cage treatment, and the random factor was the cage treatment replicate nested within field. A graphical validation procedure was applied to check that underlying statistical assumptions were not violated. Because heterogeneity was detected within residuals, the response variable was $\log(x + 1)$ -transformed to meet the assumptions of the model (Zuur *et al.* 2009).

To assess the effects of landscape complexity and crop rotation schemes on the overall biological control and the parasitism rates of aphids, we compare all possible linear models resulting from combinations of the explanatory variables. We used the first PCA axis and the average proportion of ley in the landscape between 2009 and 2011 as explanatory variables. This approach resulted in comparing five models (Four models resulting from all combinations between explanatory variables including the interaction term and the intercept model) at each spatial scale per response variable. The interaction was only included when the two explanatory variables were introduced in the models as well. The response variables were as follows: the average overall biological control, the average parasitism rates, the within-field variability in biological control and the within-field variability in parasitism rates.

For each response variable, models were compared using the second order Akaike information criterion (AIC_c), which is a bias-corrected version of the AIC (Burnham & Anderson 2002). This approach was conducted at six different spatial scales, taking into account explanatory variables computed from 0.5 km to 3 km radii. At each scale, we reported the maximum log-likelihood estimate, the Akaike weights, the AIC_c differences (Δi) and the adjusted R^2 of the 'best-fitting' models among the candidate models. Following Burnham & Anderson (2002), models with $\Delta i < 2$ were considered as competing models having substantial support for the data. To analyse the relative importance of each scale, we consider together all possible models at all scales and recomputed the Akaike weights normalized among all models (i.e. considering the min AIC_c among all models). Using Akaike weights, we were able to compute the probability that models including landscape variables at a given scale were considered as the best model among all possible models at all spatial scales. All predictors included in models had a variance inflation factor ≤ 2.2 indicating no problematic collinearity among predictors. Spatial autocorrelation in the residuals of the best-fitting models was examined using bubble plots and Moran's I statistic. No spatial autocorrelation was found in any models. For each model, a graphical validation procedure was applied to check that underlying statistical assumptions were not violated. The coefficient of variability in overall biological control was square root-transformed, and parasitism rates were arcsine square root-transformed. Statistical analyses were performed using the statistical program R, version 2.15 (R Development Core Team 2012).

Results

IMPACT OF PREDATORS ON *R. PADI*

There were no differences in number of aphids between the cage and the open treatment at the beginning of the experiment ($F_{1,75} = 0.195$, $P = 0.66$), indicating that our pairing in the field was successful (Fig. 1). There was a strong effect of natural enemies on aphid populations with significantly more aphids in the cage than in the open treatment after five days of exposure ($F_{1,75} = 81.22$, $P < 0.0001$) (Fig. 1). Aphid densities were 125% higher in the cage treatment compared with the open treatment. After five days of exposure, average reduction in aphids on open plants attributable to natural enemies was 57% (Fig. 1). Similar numbers of aphids per pot were found in the cage treatment at the beginning and at the end of the experiment and in much higher densities than initially inoculated. This indicates aphid reproduction between aphid inoculation and placement in the field and that aphid reproduction in the cage experiment after placement in the field was very low.

OVERALL BIOLOGICAL CONTROL

The mean reduction in aphid populations by natural enemies was best predicted by landscape complexity at the 0.5 km or the 1 km spatial scales (Table 1; see Table S2). At these two scales, models including the first PCA axis as the only predictor had the lowest AIC_c scores among

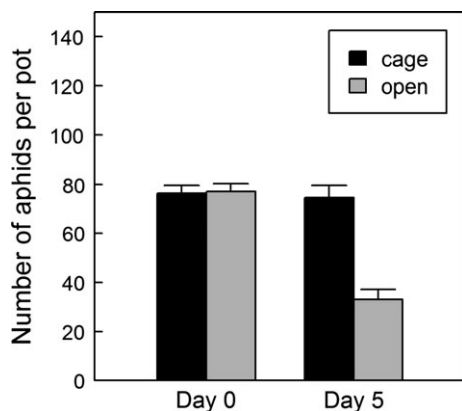


Fig. 1. Mean (\pm SE) number of aphids, *Rhopalosiphum padi*, per pot in the cage and the open treatments at the beginning (day 0) and the end (day 5) of the experiment. No significant differences were found between the two treatments at day 0, while significant differences were found between the cage and the open treatment at day 5.

their respective candidate models. These two models had the same probability (0.31, 0.29) of being selected as the best-fitting model among any potential models at all scales (Table 1). There was a significant positive relationship between the average overall biological control and the first PCA axis at these two scales (Table 1 and Fig. 2). The proportions of variance explained by these two models were similar (Table 1). Models including explanatory variables computed at scales larger than 1.5-km radius were never found to have as substantial support for the data.

VARIABILITY IN OVERALL BIOLOGICAL CONTROL

As the average proportion of ley in the landscape increased so did the within-field variability in overall biological control of aphids (Fig. 3). The variability in overall biological control was best predicted by the average proportion of ley in the landscape at a scale of 3 km. This model had the lowest AIC_c scores and had the highest

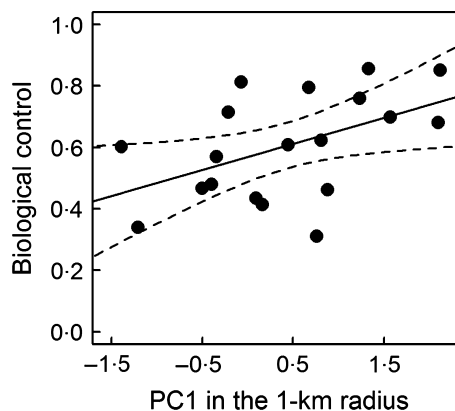


Fig. 2. Relationship between the average reduction in aphids due to natural enemies and the first PCA axis at the 1-km radius. The biological control service delivered by natural enemies was quantified as the average proportion of aphid suppression in the open treatment compared with aphid population in the cage treatment. The solid line represents the regression line; the dashed lines denote the 95% confidence interval. $y = 0.56 + 0.085x$, $r^2 = 0.24$, d.f. = 17, $P = 0.03$.

probability of being selected as the best-fitting model among any possible models at all scales (Table 2). Models including the average proportion of ley at the 2- and 2.5-km scales were also the best models among candidate models at these respective scales. Note that the intercept model was also selected as a candidate model at the 2-km scale indicating that it has substantial support for the data. Models including the first PCA axis at these scales were never found to have substantial support for the data indicating no effect of landscape complexity at 2, 2.5 and 3 km in explaining the variability in overall biological control.

PARASITISM RATES

Mean parasitism rates of aphids after five days of exposure in the crop rotation design were low (mean \pm SD: 4.1% \pm 1.8%; min.: 0.7; max.: 15.4). A total of 164 mummies were collected (hatched: 92), and three parasitoid

Table 1. Summary of model selection for predicting biological control of aphids in relation to landscape complexity and the proportion of ley in the landscape

Scale (km)	Model	LL	AIC _c	Δ_i	w_i (at each scale)	r^2	adjusted- r^2	Relative scale importance
0.5	Int. + (0.07 \pm 0.03) PC1*	9.685	-11.8	0.00	0.613	0.25	0.20	0.31
1	Int. + (0.08 \pm 0.03) PC1*	9.637	-11.7	0.00	0.621	0.24	0.19	0.29
1.5	Int.	6.992	-9.2	0.00	0.531	0.00	0.00	0.10
1.5	Int. + (0.04 \pm 0.04) PC1	7.731	-7.9	1.37	0.268	0.07	0.02	
2	Int.	6.992	-9.2	0.00	0.585	0.00	0.00	0.09
2.5	Int.	6.992	-9.2	0.00	0.556	0.00	0.00	0.09
3	Int.	6.992	-9.2	0.00	0.519	0.00	0.00	0.10

Int., intercept; LL, log-likelihood; Δ_i , AIC_c differences between model i and the most parsimonious model among all candidate models at a given scale; w_i reports the Akaike weights of the given model among all potential models at a scale. Only competing models with a $\Delta_i \leq 2$ are reported here. See text for details.

Significance of variables is indicated as follows: * $P < 0.05$.

Parameter estimates \pm SE are indicated in parenthesis.

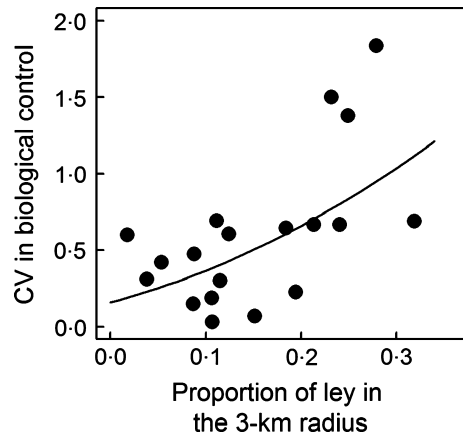


Fig. 3. Relationship between the coefficient of variation (CV) in aphid reduction and the proportion of ley at the 3-km radius. The coefficient of variation in biological control represents the within-field variability in pest control and is calculated as the standard deviation relative to the mean. Regression lines show back-transformed predictions of the most parsimonious model including ley as the only predictor.

species were found to be involved in parasitism of *R. padi*: *Praon gallicum*, *Aphidius rhopalosiphi* and *Trioxys auctus*.

We found no evidence of effects of landscape complexity or the average proportion of ley on mean parasitism rates. Indeed, we found that the null model had the lowest AIC_c scores among all possible models at each spatial scale (see Table S3). For spatial scales ranging from 1.5 to 3 km, AIC_c differences and Akaike weights provide evidence that other models including the first PCA axis or the average proportion of ley had substantial support for the data (see Table S3). This indicates a high uncertainty in model selection.

VARIABILITY IN PARASITISM RATES

The variability in parasitism rates was best predicted by the average proportion of ley at the 1-, 1.5-, 2-, 2.5- and

Table 2. Summary of model selection for predicting within-field variability (i.e. the coefficient of variation - CV) in biological control of aphids in relation to landscape complexity and the proportion of ley in the landscape

Scale (km)	Model	LL	AIC _c	Δ _i	w _i (at each scale)	r ²	adjusted-r ²	Relative scale importance
0.5	Int.	-4.237	13.2	0.00	0.617	0.00	0.00	0.05
1	Int.	-4.237	13.2	0.00	0.527	0.00	0.00	0.05
1	Int. + (0.6 ± 0.5) Ley	-3.478	14.6	1.33	0.271	0.08	0.02	
1.5	Int.	-4.237	13.2	0.00	0.388	0.00	0.00	0.05
1.5	Int. + (1.1 ± 0.7) Ley	-2.847	13.3	0.07	0.375	0.14	0.08	
1.5	Int. + (0.06 ± 0.07) PC1	-3.751	15.1	1.88	0.152	0.05	0.00	
2	Int. + (1.5 ± 0.7) Ley*	-2.051	11.7	0.00	0.516	0.21	0.15	0.11
2	Int.	-4.237	13.2	1.52	0.241	0.00	0.00	
2.5	Int. + (1.8 ± 0.7) Ley*	-1.28	10.2	0.00	0.625	0.27	0.22	0.24
3	Int. + (2 ± 0.7) Ley*	-0.576	8.8	0.00	0.652	0.32	0.27	0.48

Int., intercept; LL, log-likelihood; Δ_i, AIC_c differences between model *i* and the most parsimonious model among all candidate models at a given scale; W_i reports the Akaike weights of the given model among all potential models at a scale. Only competing models with a Δ_i ≤ 2 are reported here. See text for details.

Significance of variables is indicated as follows: *P < 0.05.

Parameter estimates ± SE are indicated in parenthesis.

3-km scales (Table 3). These models had the lowest AIC_c scores among all possible models at their respective scale. The relative scale importance indicated that the 2.5- and the 3-km radii were most important as they had the highest probabilities of being selected as the best-fitting models among any possible models at all scales (Table 3). The within-field variability in aphid parasitism rates decreased as the average proportion of ley at the 2.5- and the 3-km scales increased (Table 3; see Figure S1). Models including only the first PCA axis at any scales were never found to have substantial support for the data.

Discussion

We have, for the first time, examined the relative effects of landscape complexity and crop rotation schemes on the level and the within-field stability of natural pest control. We found that natural enemies were responsible for substantial reductions in aphid populations in spring barley fields. In particular, we found that the level of natural pest control increased with landscape complexity and that the within-field variability (at a small scale) of natural pest control decreased with crop rotation intensity in the landscape (i.e. higher variability in longer and more diversified crop rotations). Our study also revealed that variability in parasitism rates was reduced in longer and more diverse rotations. We found, in no case, interactive effects of crop rotation and habitat complexity at the landscape scale. Our results indicate that natural pest control is maximized in complex landscapes with monotonous and short crop rotations and minimized in simple landscapes with more diverse crop rotations that include perennial crops.

Our study confirms previous results using similar methodological approaches showing significant reductions in aphid populations in cereal fields from the combined action of aerial and epigeal predators (Schmidt *et al.* 2003; Holland *et al.* 2012). For instance, Schmidt *et al.*

Table 3. Summary of model selection for predicting within-field variability (i.e. the coefficient of variation - CV) in parasitism rates of aphids in relation to landscape complexity and the proportion of ley in the landscape

Scale (km)	Model	LL	AICc	Δ_i	w_i (at each scale)	r^2	adjusted- r^2	Relative scale importance
0.5	Int.	-6.564	17.9	0.00	0.52	0.00	0.00	0.00
0.5	Int. + (-0.5 ± 0.4) Ley	-5.958	19.5	1.64	0.23	0.06	0.00	
1	Int. + (-1.2 ± 0.5) Ley*	-4.240	16.1	0.00	0.49	0.22	0.17	0.00
1	Int. + (-1.5 ± 0.6) Ley* + (0.09 ± 0.07) PC1	-3.402	17.7	1.58	0.22	0.28	0.19	
1	Int.	-6.564	17.9	1.80	0.20	0.00	0.00	
1.5	Int. + (-2.2 ± 0.6) Ley**	-2.089	11.8	0.00	0.65	0.38	0.33	0.07
1.5	Int. + (-2.7 ± 0.8) Ley** + (0.09 ± 0.07) PC1	-1.331	13.5	1.74	0.27	0.42	0.35	
2	Int. + (-2.5 ± 0.6) Ley**	-1.011	9.6	0.00	0.68	0.44	0.40	0.22
2	Int. + (-3 ± 0.8) Ley** + (0.08 ± 0.07) PC1	-0.339	11.5	1.91	0.26	0.48	0.41	
2.5	Int. + (-2.8 ± 0.7) Ley**	-0.625	8.8	0.00	0.67	0.46	0.43	0.33
2.5	Int. + (-3.4 ± 0.9) Ley** + (0.08 ± 0.07) PC1	0.103	10.7	1.80	0.27	0.50	0.44	
3	Int. + (-2.8 ± 0.7) Ley**	-0.600	8.8	0.00	0.71	0.46	0.43	0.34

Int., intercept. LL, log-likelihood; Δ_i , AIC_c differences between model *i* and the most parsimonious model among all candidate models at a given scale; w_i reports the Akaike weights of the given model among all potential models at this scale. Only competing models with a $\Delta_i \leq 2$ are reported here. See text for details.

Significance of variables is indicated as follows: * $P < 0.05$, ** $P < 0.01$.

Parameter estimates ± SE are indicated in parenthesis.

(2003) found that cereal aphid populations were 172% higher when all natural enemies were removed compared with the open treatment where all predators and parasitoids had access to the aphids.

Our results support the hypothesis that landscape complexity enhances natural pest control in agroecosystems (Chaplin-Kramer *et al.* 2011). The design of our study ensured that this effect did not depend on landscape complexity being confounded with crop rotation type (cf. Persson *et al.* 2010), which has, to our knowledge, never been done before. Surprisingly, we did not find any evidence of an effect of crop rotation intensity on the mean level of pest control. Our results therefore suggest that landscape complexity is the main determinant of the level of natural pest control in our system. While the positive effect of landscape complexity on predation or parasitism rates by different taxa has been demonstrated separately in different study systems, our study shows that this relationship holds also when examining biological control resulting from the action of all natural enemies together. Östman, Ekbohm & Bengtsson (2001a), using a similar study system but only considering ground-living generalist predators, found that biological control of aphids was higher in complex landscapes early in the season during aphid establishment, whereas impact on ground-living predators was greater in more simple landscapes later in the season. Therefore, our respective results suggest that flying predators may play a significant role after aphid establishment and that taking into account flying predators strongly influence the relationship between landscape context and natural control of cereal aphids later in the season.

The level of pest control provided by natural enemies may have been enhanced in more complex landscapes

due to the higher availability of food, such as nectar, pollen and alternative prey, overwintering sites and refuges from disturbance in these landscapes (Landis, Wratten & Gurr 2000). For instance, it has been found that fecundity, body size and condition of polyphagous carabid beetles are positively correlated with landscape heterogeneity, suggesting lower food availability in homogeneous landscapes (Bommarco 1998; Östman *et al.* 2001b). Similarly, parasitoid fecundity and longevity have been found to be enhanced when supplied with nectar, suggesting higher biological control in complex landscapes supporting more abundant and diverse floral resources (Olson & Wäckers 2007). Finally, because a majority of predator species requires semi-natural habitats for overwintering, fields located in complex landscapes are assumed to support higher predator colonization rates and biological control potential (Corbett & Rosenheim 1996).

Although the level of natural pest control was not influenced by crop rotations, we found that the within-field variability of overall pest control increased with the average proportion of ley in the landscape; indicating less stability in biological control in longer and more diversified rotations. This result may be due to spillover of natural enemies between habitat types resulting from spatio-temporal variability in resource availability in the landscape. Ley is a less disturbed habitat than annual crops, providing critical food resources for natural enemies in agricultural landscapes. Bommarco (1999) compared habitat quality for the generalist carabid *P. cupreus* and found higher egg load, amount of stored fat and live body weight in carabids in ley compared with those from barley and concluded that this was mainly due to higher prey availability in

ley. Moreover, Bommarco & Fagan (2002) found that carabids moved out of barley to ley fields, especially when prey availability in barley fields was low. Other generalist predators such as spiders or staphylinids are assumed to follow the same process of landscape supplementation (*sensu* Dunning, Danielson & Pulliam 1992). Thus, the magnitude and direction of spillover effects between habitats are driven by habitat quality and spatio-temporal resource availability (Rand, Tylianakis & Tscharntke 2006). Whereas ley patches within the landscape may act as a source of natural enemies in the spring at the beginning of the aphid colonization phase, ley patches can attract generalist predators later in the season if prey populations are low in cereal fields. Our experiment took place in the summer after the aphid infestation peak and after the generalist predators' colonization phase (i.e. the ear emergence and the flowering stage). Therefore, the emigration of natural enemies from barley to ley patches due to processes of landscape supplementation may be responsible for higher variability in natural enemy densities in annual crops and thus may increase the within-field variability in pest control. Östman, Ekbom & Bengtsson (2001a) found higher predation of aphids by generalist predators in landscapes with low proportions of non-arable habitats in the later part of the season and also suggested a switch to other sources of food in complex landscapes at that time. However, other relationships between the proportion of ley and variability in biological control might occur depending on the timing of the experiment relative to prey availability in the fields and degree of food and habitat specialization of predators. Moreover, even if variation in management of conventional barley fields is expected to be low at the regional scale, the within-field variability in natural pest control might have been affected by between-field differences in farming practices. Thus, further similar experiments at different time periods during the growing season, are needed to fully understand the effect of crop rotation on the spatial variability in the delivery of natural pest control services.

Although a higher variability in overall biological control was measured in landscapes with large proportions of ley, we found a lower variability in parasitism rates in these landscapes. This result indicates that a given habitat can affect natural enemies and ecosystem services differently over time depending on species-specific life history traits and requirements. Parasitoids are specialist natural enemies and are thus very dependent on host patches within the landscape. However, the consumption of sugar-rich food such as nectar is also known to be crucial for parasitoid survival (Olson & Wäckers 2007). Thus, parasitoids usually need to exploit complementary resources that are spatially separated to complete their life cycle (i.e. landscape complementation process – Dunning, Danielson & Pulliam 1992). Ley, which is often a mix of grasses and clover, can provide a significant amount of

floral resources in the landscape. Thus, parasitoid populations could benefit from landscapes with large amounts of ley due to smaller distances between complementary resources, higher female fecundity, increased time for host-foraging and lower mortality risks during food-foraging which in turn may have reduced the within-field variability in parasitism rates in these landscapes.

In this study, we analysed the effect of landscape characteristics on the level and stability of natural pest control at six different spatial scales. We found that the level of natural pest control of aphids was best predicted by landscape complexity at the 0.5- and the 1-km scales. These results are consistent with recent studies on biological control of aphids in different systems and regions (Gardiner *et al.* 2009; Holland *et al.* 2012) and can be interpreted as the spatial scales best suited for the management of natural pest control in the landscapes of the studied region. The spatial scales which best explained the level of pest control result from the functional spatial scales of each taxa involved in the pest regulation weighed by its relative importance in controlling the aphid populations. The functional spatial scale at which a given species responds to landscape context depends on species functional traits, such as dispersal ability, and the landscape structure itself. For instance, large generalist natural enemies usually respond to landscape complexity at larger spatial scales than small specialists (Chaplin-Kramer *et al.* 2011). Thus, the spatial scale that best explained the level of biological control is strongly dependent on the pool of natural enemy species, their interaction strength with their prey, their life-history traits and the structural characteristics of the landscape. Our results indicate that the stabilizing effect of landscape composition (i.e. crop rotation within the landscape) on the natural pest control of aphids at the time of our experiment takes place at larger spatial scales than the delivery of the mean level of pest control. This suggests that spillover of natural enemies from barley to ley fields may operate at these spatial scales.

CONCLUSIONS AND IMPLICATIONS

Our study provides the first analyses of the relative influence of landscape complexity and crop rotation schemes on the level and the spatial variability of natural pest control. Our study demonstrates that combined management of semi-natural habitat and crop rotation can stabilize and enhance natural pest control services in agricultural landscapes. In contrast to our expectations, crop rotation intensity did not affect the mean level of natural control of aphids. Instead, we found that landscape complexity was the main driver of the mean level of natural control, whereas crop rotation intensity influenced the within-field stability of pest control services. These findings have important implications in terms of management options to maintain and enhance ecosystem services in agroecosystems. They

suggest that conservation of heterogeneous landscapes, characterized by higher proportion of semi-natural habitats such as pastures and relatively small fields, is essential for maintaining and enhancing effective biological control in agroecosystems. Because generalist predators are major biological control agents in all types of cereal crops, increasing the amount of pastures and field borders may also enhance natural control of pests in other cereal crops than barley. However, additional similar studies considering natural control of several pests on other crops are needed to explore potential antagonistic or synergistic effects in suppressions of different pests and to fully understand the effect of crop rotation on the variability of natural pest control services in space and time. This study also provides valuable insights on the variables and the spatial scales relevant for designing landscapes optimizing natural pest control services. Similar additional studies on other ecosystem services such as pollination, biodiversity or carbon sequestration are needed if we are to understand synergies and trade-offs in the delivery of these services and to design multifunctional agricultural landscapes.

Acknowledgements

We thank the farmers for participating in the project. We are grateful to Martin Stjernman for GIS data and to Bernard Chaubet for parasitoid identification. We also thank two anonymous reviewers and associate editor for constructive comments and suggestions on an earlier draft. This study is part of the project Sustainable Agriculture for the Production of Ecosystem Services (SAPES), supported by Formas. This research was also funded by the ERA-Net BiodivERsA, with the national funders FORMAS, Sweden, BM BF, Germany, and FWF, Austria, part of the 2010 BiodivERsA call for research proposals.

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Received 19 September 2012; accepted 21 January 2013
Handling Editor: Doug Landis

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Correlation matrix between landscape variables.

Table S2. Model selection statistics for all possible models at all spatial scale predicting biological control of aphids.

Table S3. Model selection statistics for the best models at all spatial scale predicting parasitism rates of aphids.

Figure S1. Relationship between the coefficient of variation in parasitism rates and the proportion of ley at the 2.5 km spatial scale.