Agricultural landscape simplification reduces natural pest control: a quantitative synthesis

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Abstract

Numerous studies show that landscape simplification reduces abundance and diversity of natural enemies in agroecosystems, but its effect on natural pest control remains poorly quantified. Further, natural enemy impacts on pest populations have usually been estimated for a limited number of taxa and have not considered interactions among predator species. In a quantitative synthesis with data collected from several cropping systems in Europe and North America, we analyzed how the level and within-field spatial stability of natural pest control services was related to the simplification of the surrounding landscape. All studies used aphids as a model species and exclusion cages to measure aphid pest control. Landscape simplification was quantified by the proportion of cultivated land within a 1 km radius around each plot. We found a consistent negative effect of landscape simplification on the level of natural pest control, despite interactions among enemies. Average level of pest control was 46 % lower in homogeneous landscapes dominated by cultivated land, as compared with more complex landscapes. Landscape simplification did not affect the amount of positive or negative interactions among ground-dwelling and vegetation-dwelling predators, or the within-field stability of pest control. Our synthesis demonstrates that agricultural intensification through landscape simplification has negative effects on the level of natural pest control with important implications for management to maintain and enhance ecosystem services in agricultural landscapes. Specifically, preserving and restoring semi-natural habitats emerges as a fundamental first step to maintain and enhance pest control services provided by predatory arthropods to agriculture.

Keywords: crop protection**,** biological control, arthropods intraguild predation, ecosystem services, landscape management, spatial stability

1. Introduction

Agricultural intensification since the mid-20th century has resulted in a loss of habitat heterogeneity with important implications for biodiversity and ecosystem function within agricultural landscapes (Benton et al., 2003). During this time, agricultural production increased in part by converting natural and semi-natural habitats within agricultural landscapes into arable fields and partially replacing ecological functions, originally provided by communities of beneficial organisms, with external fossil and agrochemical inputs. But this has come at the cost of negative impacts on water and soil, human and ecosystem health, biodiversity (Tscharntke et al., 2005) and thereby possibly agricultural yields (Ray et al., 2012). A healthy ecosystem and the organisms it contains underpin agricultural productivity with ecosystem services such as crop pollination, pest control, and nutrient cycling (Bommarco et al., 2013). To achieve food security and environmental well-being in the long term, we need to better understand these ecosystem services and integrate their management into modern productive and environmentally friendly crop production systems.

Control of crop pests by their natural enemies is an important ecosystem function that supports crop production and provides agriculture with a valuable, but poorly quantified, ecosystem service (Landis et al., 2008; Tschumi et al., 2015). Natural or semi-natural habitats, such as woodlands, field margins, permanent grasslands, or hedgerows, are crucial habitats for natural enemies in the agricultural landscape as they provide overwintering sites, refuge from disturbance, and alternative prey (Landis et al., 2000; Tscharntke et al., 2007; Rusch et al., 2010). Two comprehensive reviews demonstrate that landscape complexity, commonly defined as the amount of non-crop habitats in a landscape sector surrounding the crop field, generally enhance the abundance and diversity of natural enemies across a range of cropping systems and climatic conditions, but found little evidence for an effect of landscape structure on pest abundance (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). This suggests that the positive response of natural enemies may not necessarily translate into more effective pest control (Chaplin-Kramer et al., 2011). However, an important caveat is that relatively few studies have estimated the impact of natural enemies on the growth, and hence actual suppression, of pest populations along landscape complexity or intensification gradients. In the most recent comprehensive synthesis, Chaplin-Kramer et al. (2011) listed only four estimations from three studies of impacts on pest population growth along landscape gradients, and since then several more such studies have been conducted.

In addition to influencing natural enemy abundance and diversity, landscape structure may also alter natural enemy interactions and the stability of pest suppression (Martin et al., 2013; Rusch et al., 2013). Most studies that have quantified natural enemy impacts on pests consider just one or perhaps a few parasitoid or predator taxa (e.g. ground-dwelling beetles). There is a need for multi-taxa approaches taking into account the response of each guild, as well as the overall net pest suppression resulting from positive and negative interactions among guilds. It is, furthermore, poorly known how intraguild interactions might vary with landscape simplification, and how this affects the direction and strength of predator-prey interactions across landscapes.

Increasing the stability (i.e., the inverse of variability) of ecological functions over time and space is an important motivation for the integration of ecosystem services management in mainstream crop production systems (Balvanera et al., 2006; Garibaldi et al., 2011; Bommarco et al., 2013). Increased number of service-providing species in a community increases the stability of ecosystem services such as biomass production (Weigelt et al., 2008; Cardinale et al., 2012), and crop pollination (Garibaldi et al., 2011). The diversity and community composition of natural enemies can also influence the magnitude and stability of natural pest control, but the outcomes may vary. A higher diversity of natural enemies has been shown to increase overall predation rates, and to stabilize pest control through niche partitioning, facilitation, and a higher probability of having efficient predators included in a species rich community (Letourneau et al., 2009; Cardinale et al., 2012). For example, facilitation has been reported between ladybeetles and carabids leading to higher aphid suppression (Losey and Denno, 1998). However, increasing predator diversity can also strengthen negative interactions among predators, *e.g.* by intraguild predation and behavioral interference (Ives et al., 2005; Straub et al., 2008). Intraguild predation between birds and flying insects, for example, has been shown to constrain pest control in complex landscapes (Martin et al., 2013). Yet another possibility is that interactions among predators in a species-rich community leave pest control unaffected due to minimal interaction among predators, or because positive and negative interactions balance each other (Letourneau et al., 2009). A majority of the studies examining the relationships between biodiversity and ecosystem functioning address impacts on stability of functioning over time. How the stability of pest control across space, and ecosystem services in general, might change with increased biodiversity has received much less attention (Rusch et al., 2013). An analysis of how various predatory guilds affect pest population growth in contrasting environmental settings could reveal the relative and combined role of key components of diversity for functioning, and how this varies with land use (Martin et al., 2013).

We performed a quantitative synthesis of the growing field of study on natural pest control services in agroecosystems to measure the effect of landscape simplification on the magnitude and stability of natural pest control in Europe and North America. Using primary data from predator exclusion experiments that include measures of pest aphid population growth, we investigated the effect of landscape simplification on (i) the magnitude and the within-field stability of natural pest control, (ii) pest control provided by different guilds of natural enemies, and (iii) impact of interactions among guilds of natural enemies on pest population growth. We predicted that increasing landscape simplification would reduce the magnitude and the within-field stability of natural pest control and increase the level of negative interactions among guilds of natural enemies.

2. Material and Methods

2.1 Studies and datasets

Our synthesis is based on published and unpublished data from 15 studies (175 field sites) from five countries and on four crops (Table 1). All data were from manipulative experiments where ground-dwelling and vegetation-dwelling arthropod enemies were excluded from their phytophagous aphid prey with cages and compared to an open treatment. The exclusion treatments differed among studies. Some studies used two exclusion modalities (total exclusion vs. open treatment) whereas other studies used four exclusion modalities (total exclusion, exclusion of vegetation-dwelling predators, exclusion of ground-dwelling predators and open treatment) (Table 1). Experiments were generally performed in insecticide free area except for some fields in Holland et al. (2012) and in Chaplin-Kramer et al., (2012) where short persistence insecticide were used (see publications for more details). The duration of the experiment as well as the number of replicates per field also varied among studies (Table 1). However, all experiments quantified the magnitude of pest control exerted by all natural enemies, and in some cases the respective impact of vegetation-dwelling and ground-dwelling predators, by comparing growth rates of aphid populations between open and exclusion treatments.

Using regionally available digital land cover maps, we calculated the proportion of cultivated land (all type of crops) in the 1 km radius around the centre of each crop field (Table 1). This measure represents a relatively simple and robust parameter for characterizing landscape simplification (Persson et al., 2010; Roschewitz et al., 2005; Rundlöf and Smith 2006) and is often correlated with other indicators of complexity, such as habitat-type diversity (e.g., Roschewitz et al., 2005; Tscharntke et al., 2005). Moreover, this measure can also be interpreted as a more general proxy for agricultural intensification, as it is often correlated with factors such as pesticide use at the field to landscape scale (Meehan et al., 2011). The 1 km spatial extent was selected because it has been identified as a relevant scale to understand trophic interactions and population dynamics for a range of organisms including natural enemies of crop pests (Thies and Tscharntke 1999; Thies et al., 2005). Land use information was provided by each author or data owner and included all crop and non-crop habitat types. Original data sources were either digitalization based on aerial imagery and field inspection or administrative data available at national scales.

2.2 Pest control

To calculate the mean level of natural pest control for each site, we measured the difference in growth rates of aphids between the total exclusion treatment and the open treatment for all 15 datasets. Because the initial numbers of aphids as well as the duration of the experiment differed markedly among sites and studies, we calculated the aphid population rate of increase r (expressed as aphid x aphid^{-1} x day^{-1}) for each replicate of each experimental treatment,

$$r = [\ln(N_t + 1) - \ln(N_0 + 1)]/t$$

where N_0 = initial number of aphids, N_t = number of aphids at time t and t = the duration of the experiment in days. This calculation allows for comparisons among sites and studies (McCallum 2000; Costamagna et al., 2007; Latham and Mills 2010). For each replicate at each site, the difference in the rate of increase (between the total exclusion treatment and the open treatment) reflects the net mortality of aphids. Based on our experimental design, this mortality is assumed to be mainly due to natural enemies. In addition, we analyzed the spatial variation in the level of aphid control exerted by all natural enemies per site using the coefficient of variation (CV) calculated by dividing the standard deviation of the sample with its mean (Garibaldi et al., 2011). This allows us to explore how the within-field stability in pest control is affected by landscape simplification.

To distinguish between the magnitude of pest control provided by ground-dwelling predators alone, or by vegetation-dwelling predators alone, we used a subset of seven datasets where either ground-dwelling, or vegetation-dwelling predators were partially excluded. We calculated the differences in aphid growth rates between the total exclusion and partial exclusion treatments for each replicate at each site, and calculated the CV for each site.

Finally, to characterize interactions between ground-dwelling and vegetation-dwelling predators, we calculated the difference between the overall pest control exerted by all natural enemies (using the open and total exclusion treatments), and the sum of pest control by ground-dwelling predators only, and vegetation-dwelling predators only (using the partial exclusion, and total exclusion treatments respectively). A positive result, with a higher overall pest control than the additive effect of control exerted by ground-dwelling and vegetation-dwelling predators, indicates facilitation between ground-dwelling and vegetation-dwelling predators. For instance, higher predation rates of aphids by carabids were found in the presence of ladybeetles due to increased number of living aphids falling to the ground due to ladybeetle foraging (Losey and Denno, 1998). A negative result indicates that there are negative interactions among predators in the community, such as intraguild predation, or behavioral interactions. For instance, a recent study reported high levels of spider predation by carabids in winter wheat fields and clear evidence of prey choice (Davey et al., 2012).

2.3 Statistical Analyses

Linear mixed models were used to evaluate the effects of landscape simplification within a 1 km radius on several response variables: the mean level of overall natural pest control (calculated as the mean difference in the rate of increase *r* between exclusion and open treatment per site) and its within-field stability (calculated as the CV per site), the mean level of natural pest control by vegetation-dwelling and ground-dwelling natural enemies and their within-field variability, and the type and amount of interactions between vegetation-dwelling and ground-dwelling predators. In each model, the proportion of cultivated land in a 1 km radius around the study site was included as a fixed effect. For each response variable, we fitted a random intercept and slope model which included datasets as a random effect and allowed each datasets to have a unique intercept and a unique slope. Dataset defined here a set of field experiments performed in a given location in a given year (see Table 1). The overall slope of the model represents a weighted average over studies, where the relative influence of a study increased with the precision of each studies' model fit and sample size. To quantify the variation among studies in the influence of the fixed landscape effect on each response variable, we estimated intercepts and slopes for each study (Qian et al., 2010). Normality and homoscedasticity assumptions were assessed using graphical tools and these assumptions were valid in all models. Statistical analyses were performed using the statistical program R, version 2.15 (R Development Core Team 2012) and the lme4 package (Bates et al., 2015).

3. Results

The mean level of natural pest control decreased linearly with the proportion of cultivated land in the surrounding landscape ($F_{1,157} = 9.77$, $P = 0.002$, Figure 1). A simplification of the landscape from 2% to 100% of cultivated land reduced the level of aphid control by about 46 % (Figure 1). Estimated slopes for individual studies were consistent with this pattern (Figure 1). The proportion of cultivated land in the 1 km radius did not affect the within-field spatial variation in the overall level of natural pest control ($F_{1,136} = 0.25$, $P = 0.61$) (Figure S1).

Analyses of a subset of seven datasets that used partial exclusion experiments revealed that the proportion of cultivated land in a 1 km radius did not affect aphid control by ground-dwelling predators ($F_{1,58} = 0.06$, $P = 0.79$), or vegetation-dwelling predators ($F_{1,58} = 0.0007$, $P = 0.97$). Similarly, the proportion of cultivated land in the 1 km radius did not affect the within-field spatial variation in aphid control resulting from ground-dwelling ($F_{1,58} = 1.42$, $P = 0.23$), or flying predators ($F_{1,58} = 0.87$, $P = 0.35$) (Figure S2 and S3).

We found both positive and negative interactions among predators (Figure 2). The proportion of cultivated land in the 1 km radius did not affect the level of interactions between ground-dwelling and vegetation-dwelling predators ($F_{1,58} = 0.65$, $P = 0.42$) suggesting little interaction among predators, or a balance between negative and positive interactions in the community. Estimated slopes for individual datasets were consistent with this pattern (Figure 2).

4. Discussion

Although it is well recognized that populations of natural enemies are strongly influenced by landscape context (Bianchi et al., 2006; Tscharntke et al., 2007; Chaplin-Kramer et al., 2011), our study is the first quantitative analysis assessing the effect of landscape simplification on natural pest control and natural enemy interactions based on experimental exclusion approaches. We found a negative effect of landscape simplification within a 1 km radius on the magnitude of pest control by natural enemies, but detected no influence of landscape simplification on the within-field variability of pest control. The negative relationship between landscape simplification and overall natural pest control was consistent across crops and countries, suggesting that landscape simplification generally reduces top-down control. Our results complement recent findings where both generalist and specialist enemies responded positively to landscape complexity in terms of abundance and diversity (Chaplin-Kramer et al., 2011). Thus, maintaining or increasing natural and semi-natural habitat in the landscape both benefit natural enemies and lead to higher effective pest control.

While the positive effect of landscape simplification on natural pest control by some guilds, such as parasitoids, has been previously suggested (Thies and Tscharntke 1999; Bianchi et al., 2005), these results indicate that this relationship holds at the community level when examining the overall top-down control resulting from the combined effects of all arthropod enemies on pest populations. The fact that a relative increase of cultivated land from 2% to 100% in the 1 km radius (based on combined datasets) reduced the level of natural pest control by about 46 % suggests that landscape is a major determinant of pest control functioning and insect pest outbreaks in agriculture (Tscharntke et al., 2005; Meehan et al., 2011). Factors leading to reduced natural pest control in simplified landscapes may include the lower availability of alternative hosts or prey, and of overwintering habitats and refuges from disturbance for natural enemies (Landis et al., 2000; Tscharntke et al., 2007, Schellhorn et al., 2015). Moreover, other aspects of agricultural intensification that are correlated with landscape structure, such as pesticide use, can add pressure on natural enemies and reduce pest control in simplified landscapes (Meehan et al., 2011).

The hypothesis that more simple landscapes strengthen negative interactions among natural enemies was not supported. There were similar occurrences of negative and positive interactions along the landscape simplification gradients. Although simple landscapes generally support less diverse and abundant communities of natural enemies (Chaplin-Kramer et al., 2011), this result suggests that negative interactions between predators may also occur in species-poor communities. Further, investigations will be needed to understand the relationships between predator community structure and the occurrence and strength of negative interactions.

Surprisingly, landscape simplification did not affect the within-field variability in overall natural pest control. Stability of ecosystem functions is thought to increase with species richness due to niche complementarity, facilitation, or sampling effects (Hooper et al., 2005); a positive relationship that has been found for a variety of ecosystem functions including biomass production, crop pollination, and pest control (Garibaldi et al., 2011; Isbell et al., 2009; MacFadyen et al., 2011). Studies linking natural enemy diversity to pest control services have focused on temporal stability, while spatial stability remains largely unexplored although considerable spatial heterogeneity in terms of abundance of natural enemies and their prey have been observed within fields (Holland et al., 2004; Winder et al., 2005; MacFadyen et al., 2011). Because landscape complexity is known to enhance natural enemy diversity and abundance, we expected to find a lower within-field stability (higher variability) in pest control in simple compared with more complex landscapes. The lack of this relationship in our study might be a result of the low number of within-field replicates and the limited duration of experiments used to measure pest control (five to 14 days for CV in pest control). This time span might be sufficient to detect landscape effect on pest control due to higher abundance of natural enemies, but too short to detect complementarity effects emerging from species-rich assemblages.

We found an effect of the proportion of cultivated land on the level of natural pest control by all natural enemies, but not on the level of pest control by ground-dwelling and vegetation-dwelling predators alone. This may be due to the relative importance of natural enemy guilds varying among regions (Thies et al., 2011) making general effects of landscape simplification on each guild difficult to perceive. Moreover, the scale and the habitat characteristics affecting each guild might vary considerably, making it more challenging to detect any effect of landscape simplification on a subset of seven case studies.

The aim of this study was to synthesize the knowledge about the effect of landscape simplification on natural pest control services. However, all the cage experiments used aphids as a model system because they are major pest for numerous crops, have relatively low mobility during the growth phase, and are known to be consumed by a variety of enemies (Schmidt et al., 2003; van Emden and Harrington, 2007). To enable broader conclusions on effects of land use on natural pest control, future experimental assessments need to consider additional predator and pest taxa with different functional attributes and life cycle requirements. Moreover, the density of prey occurring in fields may be another important determinant of the level of pest control, affecting the population dynamics of natural enemies and the services they deliver (Costamagna et al., 2004; Rusch et al., 2015), and should be taken into account in future study.

In conclusion, our analysis revealed that landscape simplification reduced levels of natural pest control irrespective of positive or negative interactions among natural enemies. These findings affirm that conserving natural habitat or re-diversifying agricultural landscapes using natural or semi-natural habitats provides viable control of crop pests that can be further supported and complemented with more directed measures (Schellhorn et al., 2015).

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Table 1: Summary of the exclusion experiment studies for the quantitative synthesis on the effect of landscape simplification on natural pest control.

Study code	Crop	Prey species	Exclusion treatment: open & total exclusion	Exclusion treatment: open, partial & total exclusion	Duration of the experiment	Location	Number of fields	Replicates per field	Landscape gradient (range of % of cultivated land in 1 km radius)	References
Study 1a	*Brassica oleracea*	*Brevicoryne brassicae* (Linnaeus)	Yes	No	12 days	USA, California	9	3	02 - 94 %	Chaplin-Kramer and Kremen (2012)
Study 1b	*Brassica oleracea*	*Brevicoryne brassicae* (Linnaeus)	Yes	No	12 days	USA, California	10	2	02 - 94 %	Chaplin-Kramer and Kremen (2012)
Study 1c	*Brassica oleracea*	*Brevicoryne brassicae* (Linnaeus)	Yes	No	12 days	USA, California	10	2	02 - 94 %	Chaplin-Kramer and Kremen (2012)
Study 2	*Triticum aestivum*	*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)	No	Yes	13 or 14 days	Germany, Göttingen	8	2	26 - 93 %	Thies et al., (2011)
Study 3a	*Triticum aestivum*	*Sitobion avenae* (Fabricius)	No	Yes	14 days	UK, Dorset and Hampshire	14	2	33 - 87 %	Holland et al., (2012)
Study 3b	*Triticum aestivum*	*Sitobion avenae* (Fabricius)	No	Yes	14 days	UK, Dorset and Hampshire	12	2	27 - 87 %	Holland et al., (2012)
Study 4	*Triticum aestivum*	*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)	No	Yes	11 - 23 days	Germany, Jena	8	2	48 - 98 %	Thies et al., (2011)
Study 5	*Triticum aestivum*	*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)	No	Yes	16 - 19 days	Poland	8	2	39 - 94 %	Thies et al., (2011)
Study 6	*Hordeum vulgare*	*Rhopalosiphum padi* (Linnaeus)	Yes	No	5 days	Sweden, Scania	31	4	14 - 88 %	Rusch et al., (2013) ; unpublished data
Study 7	*Hordeum vulgare*	*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)	No	Yes	20 - 22 days	Sweden, Uppsala	8	2	56 -100 %	Thies et al., (2011)
Study 8	*Hordeum vulgare*	*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)	No	Yes	21 - 27 days	Sweden, Scania	8	2	48 - 100 %	Winqvist C. unpublished data
Study 9a	*Glycine max*	*Aphis glycines* (Matsumura)	Yes	No	7 - 14 days	USA, Michigan	12	4	9 - 79 %	Woltz et al., (2012) ; unpublished data
Study 9b	*Glycine max*	*Aphis glycines* (Matsumura)	Yes	No	7 - 14 days	USA, Michigan	12	4	16 - 89 %	Woltz et al., (2012) ; unpublished data
Study 10a	*Glycine max*	*Aphis glycines* (Matsumura)	Yes	No	14 days	USA, Michigan, Wisconsin, Iowa, Minnesota	12	4	39 -92 %	Gardiner et al., (2009)
Study 10b	*Glycine max*	*Aphis glycines* (Matsumura)	Yes	No	14 days	USA, Michigan, Wisconsin, Iowa, Minnesota	13	4	32 - 97 %	Gardiner et al., (2009)

Figure legends

Figure 1: Mean level of overall natural pest control in relation to the proportion of cultivated land in a 1 km radius around fields. The level of pest control was measured by the difference in growth rates of aphids (*r*) between the total exclusion treatment and the open treatment per day (aphid x aphid^{-1} x day^{-1}) (see text for details). On the left, each point represents a field site within a study and the line represents the overall regression estimated from the linear mixed effect model. On the right, each point represents the slope of the model for each study (grey) and overall mean slope for all models (black), resulting from the random intercept and slope model.

Figure 2: Magnitude and direction of interactions between ground-dwelling and vegetation-dwelling predators in relation to the proportion of cultivated land in a 1 km radius. On the left, each point is a field site within a study. On the right, points represent the slopes of models for each study (grey) and the overall mean (black), resulting from the random intercept and slope model. Interactions between the two functional groups were calculated as the difference between natural pest control exerted by all natural enemies, and the sum of natural control by ground-dwelling and vegetation-dwelling predators together. Positive values indicate facilitation between the two groups whereas negative values indicate negative interactions such as intraguild predation or behavioral interactions.

Figure1

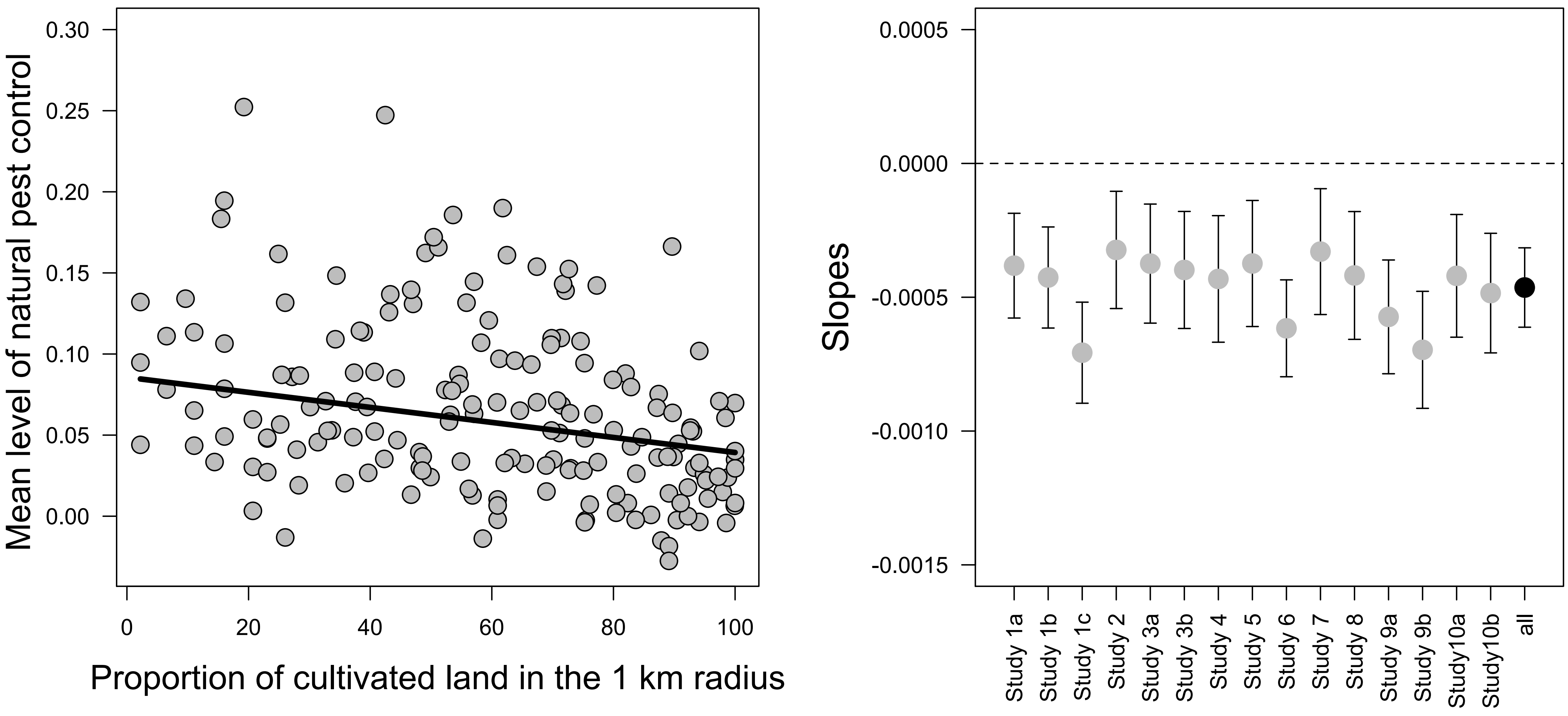
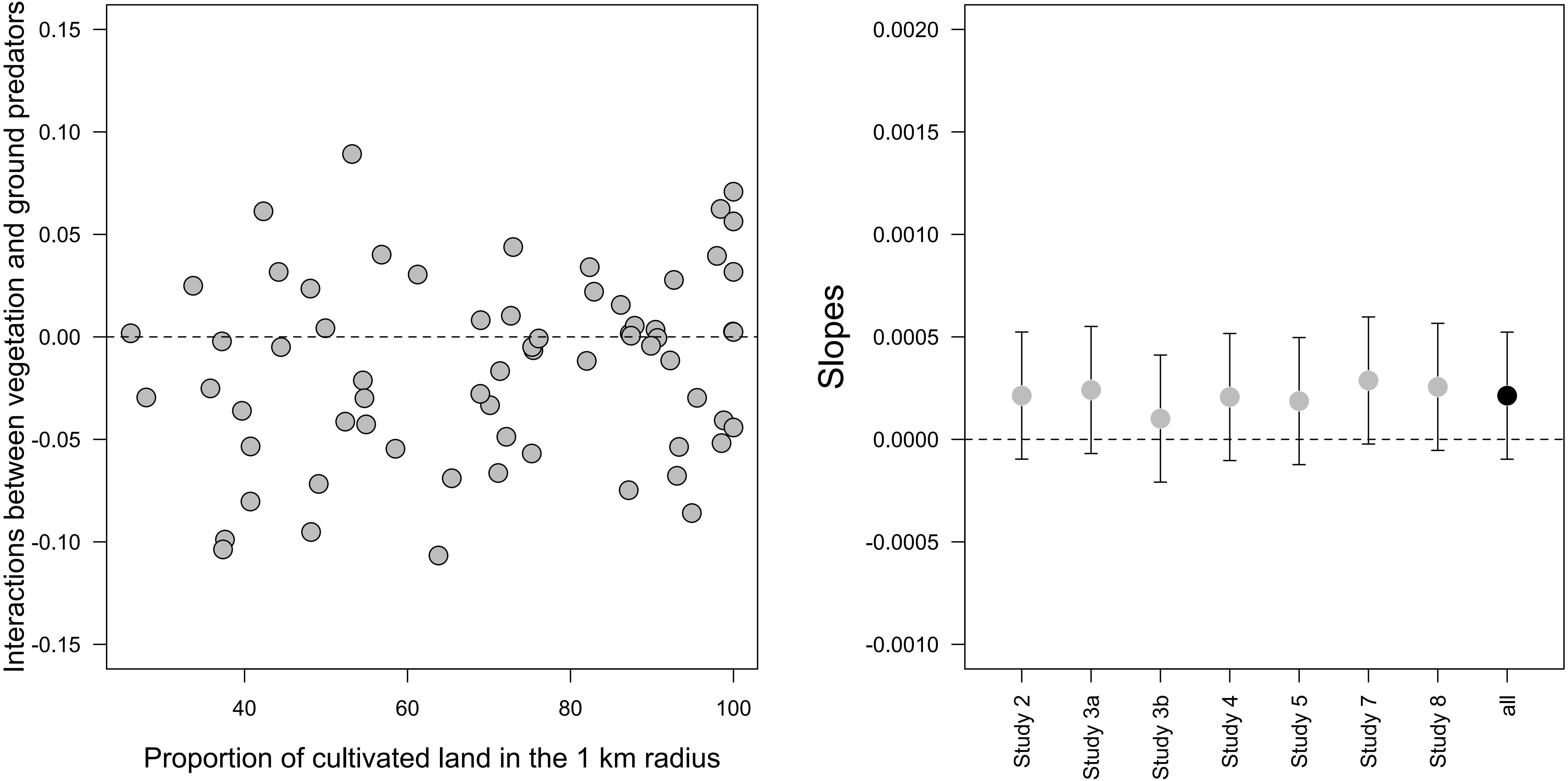

Mean level of natural pest control
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
20
40
60
80
100
Proportion of cultivated land in the 1 km radius
Slopes
0.0005
0.0000
-0.0005
-0.0010
-0.0015
Study 1a
Study 1b
Study 1c
Study 2
Study 3a
Study 3b
Study 4
Study 5
Study 6
Study 7
Study 8
Study 9a
Study 9b
Study10a
Study10b
all

Figure2


Interactions between vegetation and ground predators
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
40
60
80
100
Proportion of cultivated land in the 1 km radius
Slopes
0.0020
0.0015
0.0010
0.0005
0.0000
-0.0005
-0.0010
Study 2
Study 3a
Study 3b
Study 4
Study 5
Study 7
Study 8
all