

Ecological production functions for biological control services in agricultural landscapes

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Summary

1. Research relating to ecosystem services has increased, partly because of drastic declines in biodiversity in agricultural landscapes. However, the mechanistic linkages between land use, biodiversity and service provision are poorly understood and synthesized. This is particularly true for many ecosystem services provided by mobile organisms such as natural enemies to crop pests. These species are not only influenced by local land use but also by landscape composition at larger spatial scales.

2. We present a conceptual ecological production function framework for predicting land-use impact on biological control of pests by natural enemies. We develop a novel, mechanistic landscape model for biological control of cereal aphids, explicitly accounting for the influence of landscape composition on natural enemies varying in mobility, feeding rates and other life history traits. Finally, we use the model to map biological control services across cereal fields in a Swedish agricultural region with varying landscape complexity.

3. The model predicted that biological control would reduce crop damage by 45–70% and that the biological control effect would be higher in complex landscapes. In a validation with independent data, the model performed well and predicted a significant proportion of biological control variation in cereal fields. However, much variability remains to be explained, and we propose that the model could be improved by refining the mechanistic understanding of predator dynamics and accounting for variation in aphid colonization.

4. We encourage scientists working with biological control to adopt the conceptual framework presented here and to develop production functions for other crop-pest systems. If this kind of ecological production function is combined with production functions for other services, the joint model will be a powerful tool for managing ecosystem services and planning for sustainable agriculture at the landscape scale.

Key-words: aphid, economic value, ecosystem service, land use, model, natural enemy, pest, predator

Introduction

Sustainable agriculture requires an integration of ecosystem services into management decisions (Bommarco, Kleijn & Potts 2013). Development of biophysical models that predict ecosystem service delivery under different land-use scenarios should therefore be high on the research agenda (Daily *et al.* 2009; Nelson *et al.* 2009). Production functions have long been used in agriculture and manufacturing, where the delivery of a commodity (e.g., crop yield) is related to quantity and quality of various inputs (e.g., pesticides). This approach can be adapted to the delivery of ecosystem services through ecological production functions describing the links between land use, ecosystems and communities and delivery of ecosystem services (Daily *et al.* 2009). Recently, ecosystem services have been modelled and mapped (Jackson *et al.* 2005; Lonsdorf *et al.* 2009; Nelson *et al.* 2009). However,

our understanding of the relationship between land use, biodiversity and service provision is still limited (Nicholson *et al.* 2009), and therefore, ecological production functions tend to be simplistic. They do not, for instance, usually take into account the contribution of different components of biodiversity to ecosystem service delivery. Importantly, the predictive ability of ecological production functions is often uncertain because validation has been limited. Furthermore, key services remain to be modelled and integrated into multi-service frameworks.

Biological pest control is an ecosystem service of immense economic value provided by predators, parasitoids and pathogens (Östman, Ekbom & Bengtsson 2003; Landis *et al.* 2008; Zhang & Swinton 2012). These beneficial organisms are mobile and local delivery, for example, to a crop field, usually depends on the composition and structure of the surrounding landscape (Kremen *et al.* 2007). Complex landscapes generally harbour higher abundance and species richness of beneficial natural enemies than simple landscapes (Bianchi, Booij & Tscharntke

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2006; Chaplin-Kramer *et al.* 2011). Biological control efficacy has also been shown to be lower in fields located in landscapes simplified by intensive agriculture, compared to more complex landscapes with larger proportions of non-crop vegetation (Östman, Ekblom & Bengtsson 2001; Landis *et al.* 2008; Werling *et al.* 2011; Winqvist *et al.* 2011; Rusch *et al.* 2013).

With its long research tradition, biological control is a service for which extensive background information exists, and knowledge about different service-providing species is comparatively good. Hence, biological control is an excellent choice for exploring generalities of delivery and value of services in relation to landscape scale land use and biodiversity. Despite this, there is a surprising lack of models that predict biological control levels and stability under contrasting land uses. Several studies have modelled land-use effects on predator–prey dynamics at a local field scale (Kean *et al.* 2003; Bianchi & Wäckers 2008; Zhang & Swinton 2009) and a few have also explored how the composition and configuration of habitat types in the landscape may influence predator–prey dynamics (Bianchi & Van der Werf 2003; Bianchi *et al.* 2010). However, these studies did not attempt to predict how changes in land use influence the delivery of biological control services across real agricultural landscapes.

A challenge when developing ecological production functions for biological control is that interactions among three trophic levels need to be considered (Bahlai, Weiss & Hallett 2013). To facilitate the development of ecological production functions for biological control in different crop–pest systems, we, therefore, present a conceptual framework that describes the influence of land use on biological control and how this is mediated by biodiversity. To exemplify the production function approach, we developed a spatially explicit landscape model for a well-explored and economically important study system: biological pest control of aphids in cereals. We applied the model to a region in Sweden to predict and map biological control of cereal aphids across all spring sown barley fields in this region. Finally, we validated model results with independent data and discuss how the model can be improved.

Materials and methods

CONCEPTUAL FRAMEWORK FOR BIOLOGICAL CONTROL SERVICES

The conceptual framework for land-use effects on biological control services is inspired by a framework developed for pollination services provided by flower visiting insects (Kremen *et al.* 2007). The biological control framework incorporates, in addition, interactions among three trophic levels, where included organisms have different mobility, feeding rates and life-history characteristics both within and among trophic levels (Fig. 1). The main components of the biological control framework together with key references are briefly described as follows, where numbers in parentheses refer to links shown in Fig. 1. Changes in local management modify the landscape structure (1), and both local land use (2a–c) as well as landscape structure (3a–c) affect plant, herbivore and natural enemy communities (Landis, Wratten & Gurr 2000; Chaplin-Kramer *et al.* 2011; Winqvist *et al.* 2011). A wide range of

biotic and abiotic factors such as resource availability (Bianchi, Goedhart & Baveco 2008), pesticide applications and other disturbances (Jonsson *et al.* 2012), and changes in habitat connectivity and configuration (Perovic *et al.* 2010) will mediate changes in plant, herbivore and natural enemy communities. To maintain simplicity, the framework does not distinguish between these factors in describing the direct effect of landscape structure on the three communities; instead, an aggregate is used (3a–c; separating between these mediating factors would have required at least another 12 arrows). Because we are dealing with biological control, the crop to be protected will define the herbivores and natural enemies of interest; these target species will interact with their respective communities, possibly via competition (4a–c). Three bilateral trophic interactions are identified; natural enemies interact with herbivores (5a), herbivores interact with plants (5b) and natural enemies may also interact directly with plants (5c). The latter type of interactions not only includes omnivory but also tri-trophic interactions operating via a range of mechanisms such as herbivore induced plant volatiles, extra-floral nectar and plant structure (Janssen *et al.* 2007; Heil 2008). The crop where the biological control service is delivered is attacked by a subset of the herbivores present in the local herbivore community. These target herbivores are, in turn, attacked by a subset of the predators, parasitoids and pathogens in the natural enemy community. The combined interaction between the crop, its pest herbivores and their natural enemies results in the biological control service (5d). The magnitude and stability of this service can, for example, be expressed as a reduction in the number of pest days in the crop (Östman, Ekblom & Bengtsson 2003; Landis *et al.* 2008). This biological control service helps to reduce the negative effects of herbivory on crop yield and/or quality (6a). The biological control effect on yield and/or quality can have consequences for economics and policy (6b; Östman, Ekblom & Bengtsson 2003; Landis *et al.* 2008; Zhang & Swinton 2012), which may feedback on land use and management (7; Zhang & Swinton 2012). Finally, all these interactions are highly dependent on geographic context.

CEREAL APHID STUDY SYSTEM

To exemplify the adoption of the above described framework, we develop a production function for the biological control of aphids in spring sown cereals. The model is parameterized for the region Uppland in south-central Sweden. In Europe, the most common cereal crop is winter wheat, but spring sown varieties of barley, wheat and oats are also widespread, especially in Northern Europe. In Sweden, more than a third of all cropland was planted with cereals in 2010 and more than half of these were spring sown (530,000 ha; Anonymous 2010). Aphids are destructive insect pests on cereals, and the bird cherry-oat aphid (*Rhopalosiphum padi* L.) is a key aphid pest especially on spring-sown cereals (Leather, Walters & Dixon 1989). In Sweden, the aphid colonizes the crop during late May and early June, depending on weather and location. The colonization phase is followed by a brief phase of rapid exponential population growth by wingless aphids, continuing until about the time of crop heading, in late June or early July (Östman, Ekblom & Bengtsson 2003). After heading, aphid populations usually decline rapidly in the crop due to decreased plant quality and migration to grasslands. Direct crop losses due to aphid feeding are therefore usually not observed after this stage (Östman, Ekblom & Bengtsson 2003). Cereal aphids can also cause indirect growth losses through plant virus transmission, but this is not considered in the current version of the model.

Biological control of cereal aphids is of considerable economic value in Europe (Östman, Ekblom & Bengtsson 2003; Thies *et al.* 2011). The aphids are attacked by a complex of arthropod natural enemies,

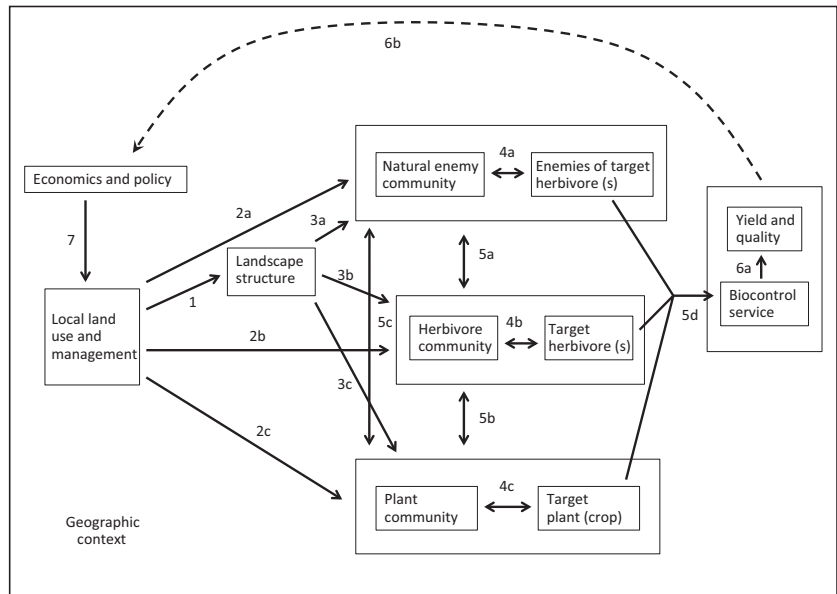


Fig. 1. Conceptual framework for the effects of land use on biological control services. Numbers refer to arrows; see text for detailed descriptions.

including generalist ground-living predators, more specialized foliage-dwelling predators that attack aphids and other soft-bodied prey and parasitoids. The most important generalist predators include wolf spiders (Araneae: Lycosidae), sheet-web spiders (Araneae: Linyphiidae), ground beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae). The generalist predators are most important during the aphid colonization phase when aphids are found at the base of the young barley plants (Wiktelius 1987), but they also contribute later in the season during the aphid population growth phase (Östman, Ekblom & Bengtsson 2001; Schmidt *et al.* 2003). Key specialists are lady beetles (Coleoptera: Coccinellidae), green lacewings (Neuroptera: Chrysopidae), hoverflies (Diptera: Syrphidae) and parasitoids (Hymenoptera: Braconidae Aphidiinae); which contribute to biological control mainly in the later population growth phase when the aphids multiply in the crop (Schmidt *et al.* 2003). The relative importance of different natural enemies varies across Europe (Thies *et al.* 2011). Parasitism is not important in the Swedish region of Uppland, for which the model is parameterized, and therefore not modelled here.

PRODUCTION FUNCTION FOR BIOLOGICAL CONTROL OF CEREAL APHIDS

The cereal aphid biological control model includes a subset of all possible interactions (3a, 5d and 6a from the conceptual framework, Fig. 1). It predicts how changes in landscape composition affect the abundance of different natural enemies (3a, Fig. 1), how this influences aphid numbers through predation (5d, Fig. 1) and ultimately contributes to reduced crop damage by the aphids (6a, Fig. 1).

We consider the aphid population during two phases: colonization (c) and exponential growth (g). The number of colonizing aphids per tiller is N_c . At the start of growth, at time 0, N_0 aphids have survived predation. After T days of growth, the population is N_T .

We express the predation mortality during phase i as

$$\mu_i = 1 - e^{-\sum_j a_{ij} P_{ij}} \tag{eqn 1}$$

where a_{ij} is the attack rate by a predator of species j on the aphids during phase i , and P_{ij} is the population density of that predator species. This function represents a functional response type I, that is, aphid *per capita* mortality rate is independent of the aphid population

size. It also means that the mortality rate increases with the predator population sizes, or to be specific, with total effective attack rate exerted by all predators acting in concert. This relation is less than linear and tends to unify as predator populations increase, that is predators compete with each other over prey. The number of aphids per tiller surviving predation during colonization and reaching the onset of growth is:

$$N_0 = N_c(1 - \mu_c). \tag{eqn 2}$$

During the phase of population growth, the aphid population grows by a rate of

$$r = f - \mu_g, \tag{eqn 3}$$

where f is fecundity, that is maximum reproductive rate under no predation and the index g refers to the population growth phase. The population size after T days is:

$$N_T = N_0 e^{rT}. \tag{eqn 4}$$

As T is only 14 days, the considered period only covers the exponential growth phase, during which growth rate can be considered independent of current population density.

Consequently, the number of aphid-days that the crop is exposed to is the integral of the population development:

$$AD = N_0 \frac{e^{rT} - 1}{r}. \tag{eqn 5}$$

Östman, Ekblom & Bengtsson (2003) found that the crop damage, due to feeding by the aphids, is a non-linear function of the number of aphid-days:

$$CD = 12 \cdot 7 AD^{0.66}. \tag{eqn 6}$$

We express the biological control effect of the predators as the relative reduction in crop damage due to the reduced aphid populations:

$$B = \frac{CD_{max} - CD}{CD_{max}}, \tag{eqn 7}$$

where CD_{max} is the maximum crop damage if no predators were present (i.e. when there is no biological control). That is, this dimensionless number estimates the relative benefit of the predators' pest control. Expression eqn 7 is equivalent to

$$B = 1 - \frac{\left((1 - \mu_c) \frac{e^{rT}}{r} \right)^{0.66}}{\left(\frac{e^{rT}}{r} \right)^{0.66}} \quad \text{eqn 8}$$

That is, the relative biological control effect is independent of the number of aphids colonizing – it is only an effect of aphid growth rates and the total mortality rates exerted by the predator communities. It should be noted that by assuming a specific aphid colonization rate, for example, estimated from previous monitoring, function (6) can also be used to predict the actual crop damage in a field.

Population sizes of some predator taxa vary with landscape characteristics. To account for non-linear threshold and saturation effects, we use non-linear sigmoid functions to model predator densities as a function of landscape variables. To maintain both flexibility and simplicity, we choose modified Gompertz-functions:

$$P_{i,j} = \hat{P}_{i,j} + a_{i,j} e^{b_{i,j} e^{c_{i,j} L_{i,j}}} \quad \text{eqn 9}$$

The population density of predator j during phase i depends on landscape variable L . This variable is the proportion of the surrounding landscape that includes the relevant land use at the relevant scale. When none of the surrounding landscape includes that land use ($L = 0$) then the predator density is $\hat{P}_{i,j}$, and it then increases or decreases with L , depending on the parameters a , b and c (Table S3). Thus eqn 9 is a generic positive or negative sigmoidal expression. It represents the phenomenological effects on the predator populations and key landscape characteristics, and the parameters are chosen so as to arrive at reasonable fit with empirical relations (Appendix S1).

MODEL PARAMETERIZATION

Aphid population model

Landscape composition was assumed not to influence the aphid colonization rate, as we found no conclusive evidence for landscape effects on *R. padi* in the literature (see Appendix S1 for further motivation). Instead, we assumed that each tiller was colonized by an average of 3.5 aphids. The fecundity of aphids (f) was 0.27 based on laboratory development rates of *R. padi* at 15 °C (Dean 1974). This temperature is close to the monthly average for the central Swedish region of Uppland in June. The length of the population growth phase (T) was set at 14 days, which is the normal time between the end of the aphid colonization phase and the time for crop heading (Östman, Ekbohm & Bengtsson 2003).

Predator abundances

We modelled abundances of the following key aphid predator groups: sheet-web spiders, wolf spiders, large and small ground beetles, rove beetles, lady beetle larvae and adults, hoverflies and green lacewings (see Appendix S1 for details). For each predator group, we first calculated the average abundance ($P_{c,j}$ and $P_{g,j}$) using data from studies conducted in Sweden in spring sown cereal crops during the two aphid population phases (Öberg & Ekbohm 2006; Thies *et al.* 2011; Caballero-López *et al.* 2012; Appendix S1; Table S1). To model landscape effects, we either used data from the literature where the relationship between the abundance of different taxa with the cover of different habitat types in the landscape surrounding the crop was studied (reviewed by Chaplin-Kramer *et al.* 2011) or we analyzed our own datasets. We considered the influence of two variables on predator abundance: the proportion of land not covered by annual crops (hereafter termed

non-crop land) and the proportion of grassland within specific landscape sectors surrounding each field. Both these variables have been found to be important for natural enemy abundance and biological control (reviewed by Bianchi, Booij & Tschamntke 2006; Chaplin-Kramer *et al.* 2011). The proportion of non-crop land was considered within radii of 135, 500 and 1500 m of each site, but for proportion of grassland within landscape sectors only a 500 m radius was used (see Appendix 1 for further motivation of the landscape variables and scales used). Each predator group was assumed to be related to a maximum of one landscape variable at each of the spatial scales for each time period (Table S1).

Per-capita predation risk

Mortality rates were determined independently for the aphid colonization phase and the aphid population growth phase ($\mu_{c,j}$ and $\mu_{g,j}$). The effect of different taxa during the two periods was parameterized by combining results from studies assessing the overall predator-inflicted mortality rates of cereal aphids during the two different phases (e.g. Östman, Ekbohm & Bengtsson 2001) and studies assessing attack rates by individual predator taxa (Freier *et al.* 1998; see Appendix S2 and Table S2 for more details).

MAPPING BIOLOGICAL CONTROL SERVICES ACROSS REAL LANDSCAPES

Modelled biological control effects were calculated from landscape variables, according to the equations above. Landscape variables were extracted from the Swedish Integrated Administration and Control System (IACS) GIS-database, provided by the Swedish Board of Agriculture and CORINE land cover data. Using this data, we can calculate an estimate of biological control effect for any point in Sweden. We did this for all 9647 barley fields in Uppland in 2009 to assess the variation in modelled biological control effect. We also did the calculations for the specific fields from which we have validation data (see below). Finally, we selected two contrasting landscapes in Uppland in 2009 yielding very low and high biological control, respectively, and calculated biological control effects on a fine scale (25 × 25 m) in all annual crop fields in these landscapes.

Sensitivity analysis

We performed a series of sensitivity analyses to examine the effects of varying aphid fecundity, overall predator abundances, attack rates and landscape effects on predator abundances. We compared fields in landscapes that showed comparatively high and low levels of biological control in the original simulations. Details of the sensitivity analysis are presented in Appendix S3.

VALIDATION OF THE BIOLOGICAL CONTROL MODEL

We used a dataset assessing the impact of predators on aphid populations in different landscapes (Östman, Ekbohm & Bengtsson 2001, 2003) to validate the model. This included estimates of overall predation rates during the aphid colonization phase, the effect of ground-living predators (primarily spiders and predatory beetles) on aphid population growth and the estimated levels of crop damage (yield loss) with and without predators in ten spring sown barley fields in Uppland in 1999. Thus, we calculated expected mortality during colonization, according to the model, and used Pearson correlation to test how well it predicted

actual measured mortalities during colonization. Similarly, we compared predicted and actual mortality during the growth phase by ground-living predators, and predicted the actual biological control effect. This was done for 10 fields, but one of them had missing data for the colonization phase.

Results

BIOLOGICAL CONTROL SERVICE POTENTIAL ACROSS LANDSCAPES

The model predicted that the biological control effect would vary between 0.47 and 0.70 among the spring sown barley fields cultivated in Uppland 2009. The effect was predicted to be higher in landscapes with a high proportion of land not covered by annual crops (non-crop land) and with a high proportion of grassland at all spatial scales considered (Figs 2 and 3). However, especially at 500 m and 1500 m radii, variability in biological control increased among fields with increasing area of non-crop land. Individual fields with no other annual crop fields in the surrounding landscape ranged between 0.47 and 0.70 in biological control effect, whereas fields embedded in landscapes with >80% annually tilled fields ranged between 0.47 and 0.55 (Fig. 3).

Adult lady beetles were the predator group with the largest predicted contribution to the biological control effect in almost all landscapes (Fig. 4). Wolf spiders, sheet-web spiders and large ground beetles also contributed significantly to the biological control effect, but their relative importance varied depending on landscape composition. The remaining predator taxa modeled i.e., hoverflies, lacewings, lady beetle larvae, small ground beetles and rove beetles each contributed less

than 0.05 to the biological control effect in all landscapes (data not shown). When all landscape variables except one were fixed to average values for the fields in Uppland, there was a positive relationship between the proportion of non-crop land at 135 m and 1500 m radii and between the proportion grassland at 500 m radius and the biological control effect. Nonetheless, there was a weak negative relationship between the proportion of non-crop land within 500 m radius and the biological control efficacy (Fig. 4). These landscape effects were largely driven by three different taxa; the positive effects of non-crop land at 135 m and 1500 m radii was driven primarily by wolf spiders and sheet-web spiders, respectively, whereas both the negative effect of non-crop land and the positive effect of grassland at 500 m radius was mainly driven by large ground beetles (Fig. 4).

Sensitivity analysis

Varying aphid fecundity, overall predator abundances and attack rates affected the biological control effect, but had little influence on the relative differences between landscapes with high and low levels of biological control. The model predictions were more sensitive to changing the predators' landscape relations, but, with few exceptions, did not dramatically alter the overall patterns generated by the model (see Appendix S3 and Figs S1–S15 for details).

MODEL VALIDATION

The mortality rate during colonization in Uppland as reported by Östman, Ekblom & Bengtsson (2001) was predicted well by our model (Fig. 5a; $r = 0.70$, d.f. = 7, $P = 0.04$). However, the

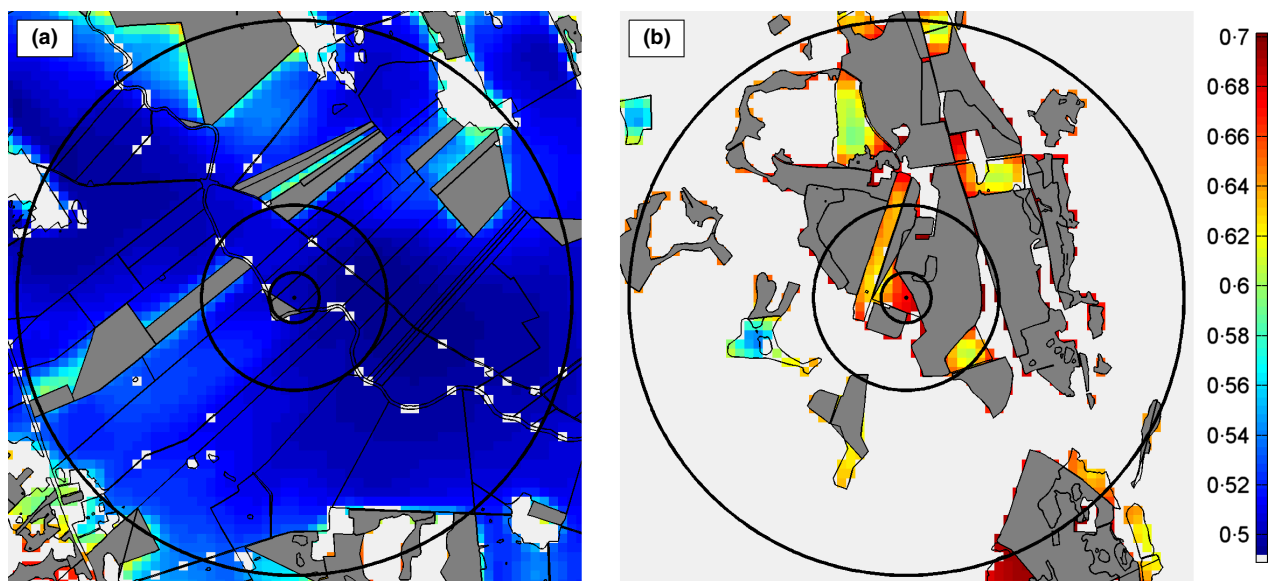


Fig. 2. Predicted biological control effects in two contrasting landscapes in the Swedish region of Uppland. Dark grey areas represent grasslands such as ley and permanent pastures, and light grey patches are non-crop habitats other than grasslands, primarily forest. Annual cropland is marked with a gradient from dark blue to dark red, depending on the predicted biological control effect. Landscape (a) is dominated by annual crops, whereas landscape (b) has a larger proportion of grassland and non-crop habitats. The concentric circles represent the three different spatial scales around a field within which landscape composition affects the biological control effect (135 m, 500 m and 1500 m radius).

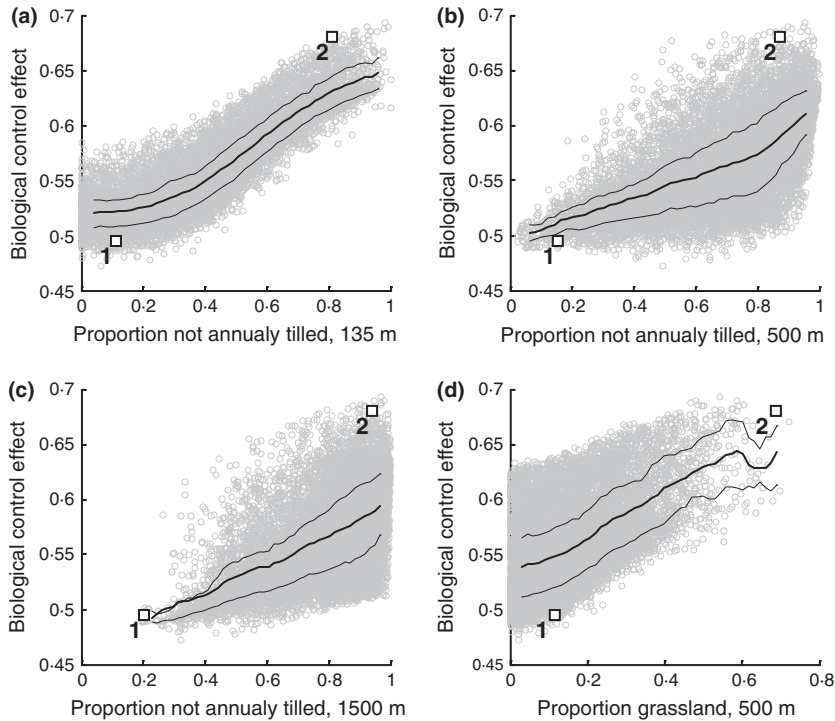


Fig. 3. Predicted biological control effect in all fields with spring-sown barley in the region of Uppland in 2009, in relation to the proportion of not annually tilled land (non-crop land) within (a) 135 m radius, (b) 500 m radius, (c) 1500 m radius, and in relation to (d) proportion of grassland within 500 m radius of a specific point in a field. (1) and (2) show the landscape composition around the field at the centre of the circles in the two contrasting landscapes in Fig. 2.

model was not able to predict the mortality rate due to ground-living predators during the growth phase of the same data (Fig. 5b; $r = 0.40$, d.f. = 8, $P = 0.3$). The model prediction for the overall biological control effect for the Uppland data was positively correlated with that estimated from data, but not significantly so (Fig. 5c; $r = 0.54$, d.f. = 8, $P = 0.1$).

Discussion

We have developed a framework for biological control production functions and, based on this, built a model for biological control of an aphid pest in cereals. One of the most important features of the framework and our example model is the incorporation of information about crop damage and potential yield reductions. This allows for the model to be combined with socio-economic models, whereby the loop described in the framework, from land use and management to service delivery, its consequences for yields, economy and policy and the potential feedbacks on land use and management can be modelled for different land-use scenarios (e.g., Brady *et al.* 2012). In addition, such production functions can be combined with models describing crop growth and might then support the development of novel crop production systems that better exploit available ecosystem services. Finally, the framework provides a basis for developing biological control models that can be integrated with natural capital models for mapping, planning and identifying synergies in the generation of multiple services across agricultural landscapes (e.g. Kareiva *et al.* 2011).

The aphid model was able to predict a significant proportion of the variation in the biological control effect in the independent dataset available for validation. It was well able to

forecast the biological control exerted by ground-living predators during the aphid colonization phase, but was less successful at forecasting and seemed to underestimate biological control during the aphid population growth phase. The model predicted that the biological control effect would be higher in complex landscapes with a high proportion of non-crop habitats and grassland. This is in accordance with other studies that have assessed biological control in relation to landscape composition in agroecosystems (Thies & Tscharrnke 1999; Landis *et al.* 2008; Werling *et al.* 2011; Winqvist *et al.* 2011; Rusch *et al.* 2013). However, the predicted variability in biological control effect in relation to landscape composition was high, despite the considerable influence of landscape on natural enemy abundance in the model. Thus, even if many empirical studies demonstrate that landscape complexity has a strong positive impact on predator abundances, this does not necessarily result in a strong relationship between landscape composition and biological control efficacy. This might explain the often observed weak or absent landscape effects on pests (Chaplin-Kramer *et al.* 2011).

In real landscapes, strong autocorrelations in landscape composition among spatial scales can override effects of landscape composition at any single scale. The model predicted a negative relationship between the proportion of land not covered by annual crops within 500 m radius, and the biological control effect in theoretical landscapes, where all other landscape parameters were set at average values for Uppland. This was due to the negative effect that non-crop land has on ground beetle abundance in this ecosystem (Winqvist *et al.* 2011). In contrast, when the model was adapted to predict biological control in real landscapes, a positive effect of the proportion of non-crop land was found at the same scale. This

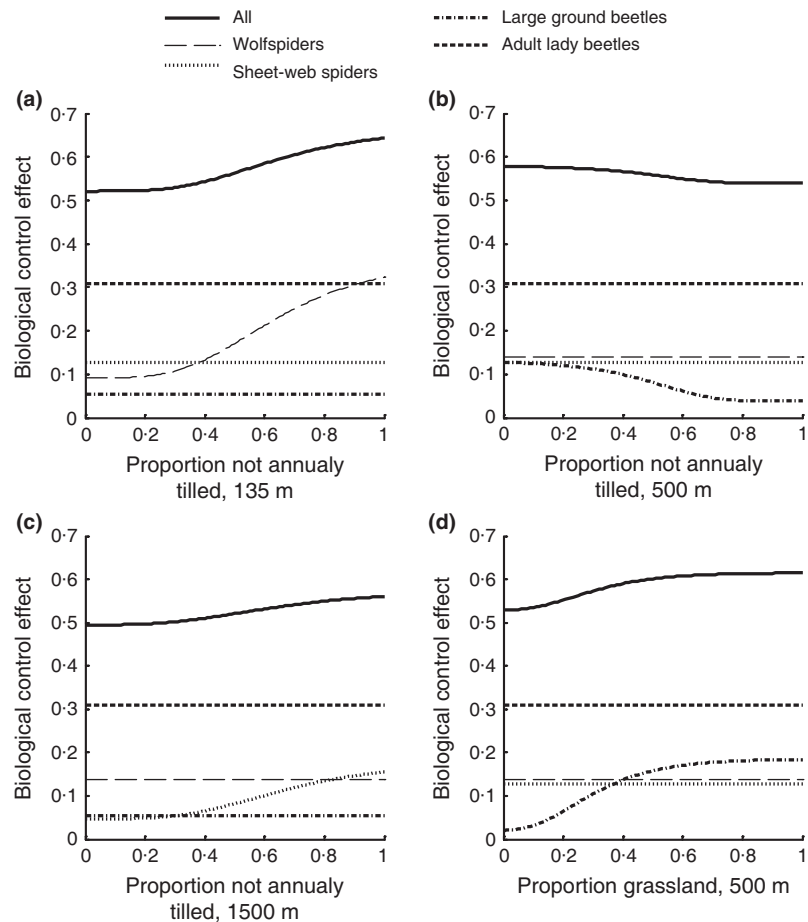


Fig. 4. Contribution of different predator taxa to the biological control effect in relation to the proportion of not annually tilled land (non-crop land), within (a) 135 m radius, (b) 500 m radius, (c) 1500 m radius, and in relation to (d) proportion of grassland within 500 m radius of a specific point in a field. Only one landscape parameter was varied at a time, with the other set at average values for all spring-sown barley fields in Uppland. Only the four taxa contributing most to the biological control effect are shown, together with the total biological control effect with all predator taxa present (all). The remaining predator taxa modelled each contributed less than 0.05 to the biological control effect in all landscapes.

was due to autocorrelations of landscape composition with other spatial scales, where positive relationships between non-crop land and biological control were caused by wolf spiders and sheet-web spiders.

There are many ways in which the predictive power of the model might be improved, and this exercise has helped us identify knowledge gaps. Firstly, we accounted for multiple spatial scales by analyzing effects of landscape sectors with different radii (Thies, Steffan-Dewenter & Tscharntke 2003; Gardiner *et al.* 2009a, b). Distance-weighting functions have recently been proposed to account for the effect of landscape composition in spatially autocorrelated landscapes (Henry *et al.* 2012). This approach would avoid the somewhat subjective selection of radii for the different landscape sectors. Secondly, the model was based on correlations between predator abundance and two rather rough estimates of landscape composition: proportion of land not covered by annual crops and grassland within a certain radius (corresponding to path 3a in the conceptual model, Fig. 1). Even though the relationships between landscape composition and predator abundances assumed are all supported by empirical studies and are reasonable from a biological point of view (see Supporting Information), they tell us little about the actual mechanisms driving the observed correlations between predator abundances and landscape parameters. Landscape effects on predatory arthropod abundances may ultimately be caused by availability of key resources such

as alternative food or hibernation sites; by variation in disturbance regimes such as insecticide application, harvest and ploughing; and by the detailed spatial relationship between habitats affecting movement. The mechanisms that drive the influence of landscape on predator communities need to be further disentangled in order to improve model predictions (Jonsson *et al.* 2012).

Thirdly, the aphid attack rates of different predators included in the model (path 5d) are, to a large extent, based on laboratory studies under simplified, artificial conditions. In reality, many of the modelled aphid predators are generalist in terms of food choice, and their frequency of aphid feeding is highly dependent on ecological context; with factors such as availability of different food types (Robinson *et al.* 2008; Kuusk & Ekbom 2012; paths 4a, 5a), intra-guild interactions and the structural complexity of habitats (Janssen *et al.* 2007; paths 4a and 5c) being important. Fourthly, we disregard effects of differences in local conditions among fields (paths 2a–c). In reality, a range of within field management measures such as insecticide application, weed management, fertilization and soil tillage can have a strong impact on both aphid and predator population dynamics (Thorbek & Bilde 2004; Krauss *et al.* 2007). Also, the effects of local management on predators may depend on landscape composition, where local impacts often are stronger in simplified compared to more complex landscapes (Thies & Tscharntke

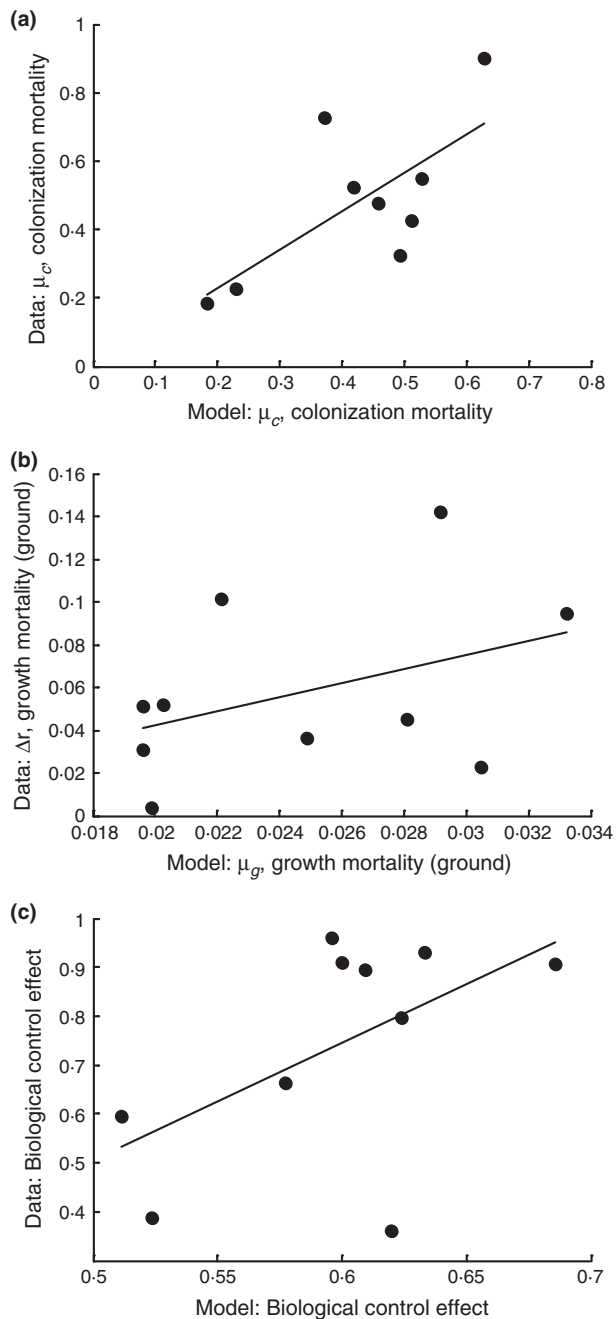


Fig. 5. Validation of the model with one independent dataset from the region of Uppland. This includes (a) overall predation rates during the aphid colonization phase, (b) the effect of ground-living predators on aphid population growth and (c) the estimated biological control effect over the whole aphid population cycle.

1999; Schmidt *et al.* 2005; Haenke *et al.* 2009; but see Winqvist *et al.* 2011).

Finally, we model biological control as a proportional reduction in yield loss due to aphids, rather than predicting the actual aphid abundance. To predict aphid abundance, we would also need to model colonization rates of aphids, which are known to vary considerably among years and regions (Bommarco, Wetterlind & Sigvald 2007). In the current model, predation rates were parameterized based on data from a

number of studies with different aphid abundances, ranging from low (0.3 aphids per tiller) to high (40 aphids per tiller; Appendix 2). The current model might therefore provide a reasonable prediction of biological control effects at sites within this range of aphid abundances, but be less effective at predicting biological control at sites with very low or very high aphid infestations. Future versions of the model should test if incorporating density dependent predation rates (Functional response II or III) and predator aggregation to fields with high aphid abundances improves model reliability.

Conclusions

To permit generalization to multiple landscapes and future conditions, ecological production functions should be based on thorough knowledge of the ecological processes generating them. A conceptual framework for the ecosystem service of biological pest control is presented and an ecological production function for cereal aphid biological control is developed. This model is based on our empirical understanding of how different predator taxa are affected by landscape level land use and how they contribute to the reduction of damage by aphids. The model was able to predict a significant proportion of the variation in biological control taking place in cereal fields from independent data. Although much variability remains to be explained, our model provides a promising starting point. We encourage the adoption of the conceptual framework presented here and the development of production functions that synthesize available knowledge in other crop-pest systems. For example, Bahlai, Weiss & Hallett (2013) presented a mechanistic model for predicting tritrophic level interactions in the soybean aphid system, and they used this model to simulate how variation in climate, natural enemy abundance and planting date would affect pest control. If this model is expanded to incorporate the effects of habitat management (Costamagna & Landis 2006) and/or landscape composition (Gardiner *et al.* 2009a, b), it could provide a further production function that can be used for mapping biological control services under different management scenarios. Such a production function can be combined with production functions for other ecosystem services, with crop growth models and socio-economic models, and become powerful tools for guiding the management of natural capital in general and the development of sustainable agriculture in particular.

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Supporting Information

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

Appendix S1. Parameterization of abundances and landscape effects.

Appendix S2. Parameterization of predation rates.

Appendix S3. Sensitivity analyses.

Table S1. Landscape effects on the abundance of different predator groups used in the model parameterization.

Table S2. Predator attack rates for different predator taxa used in the model.

Table S3. Parameters used in eqn 9: $P_{i,j} = \hat{P}_{i,j} + a_{i,j}e^{b_{i,j}\epsilon_{ij}^{L_{ij}}}$.

Figure S1. Results of a sensitivity analysis varying aphid fecundity from half to double the value used in the original simulation.

Figure S2. Results of a sensitivity analysis varying predator population sizes by a constant that ranged from 0 to 2, so that all predator species had the same proportional increase or decrease.

Figure S3. Results of a sensitivity analysis varying predator attack rates by a constant that ranged from 0 to 2, so that all predator species had the same proportional increase or decrease.

Figure S4. Results of a sensitivity analysis removing the relation of wolf spiders to proportion of land not covered by annual crops in a 135 m radius.

Figure S5. Results of a sensitivity analysis adding the relation of wolf spiders to proportion of land not covered by annual crops in a 135 m radius also to sheet-web spiders.

Figure S6. Results of a sensitivity analysis adding the relation of wolf spiders to proportion of land not covered by annual crops in a 135 m radius also to large ground beetles.

Figure S7. Results of a sensitivity analysis adding the relation of wolf spiders to proportion of land not covered by annual crops in a 135 m radius also to adult lady beetles.

Figure S8. Results of a sensitivity analysis removing the relation of sheet-web spiders to proportion of land not covered by annual crops in a 1500 m radius.

Figure S9. Results of a sensitivity analysis adding the relation of sheet-web spiders to proportion of land not covered by annual crops in a 1500 m radius also to wolf spiders.

Figure S10. Results of a sensitivity analysis adding the relation of sheet-web spiders to proportion of land not covered by annual crops in a 1500 m radius also to large ground beetles.

Figure S11. Results of a sensitivity analysis adding the relation of sheet-web spiders to proportion of land not covered by annual crops in a 1500 m radius also to adult lady beetles.

Figure S12. Results of a sensitivity analysis removing the relation of large ground beetles to proportion of land not covered by annual crops in a 500 m radius, and to proportion of grassland in a 500 m radius.

Figure S13. Results of a sensitivity analysis adding the relation of large ground beetles to proportion of land not covered by annual crops in a 500 m radius, and to proportion of grassland in a 500 m radius, also to wolf spiders.

Figure S14. Results of a sensitivity analysis adding the relation of large ground beetles to proportion of land not covered by annual crops in a 500 m radius, and to proportion of grassland in a 500 m radius, also to sheet-web spiders.

Figure S15. Results of a sensitivity analysis adding the relation of large ground beetles to proportion of land not covered by annual crops in a 500 m radius, and to proportion of grassland in a 500 m radius, also to adult lady beetles.