Biological control as an ecosystem service: partitioning contributions of nature and human inputs to yield

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Abstract. 1. The concept of ecosystem services (ES) has rapidly entered policy and planning agendas nationally and globally. However, its usefulness is hampered by, for example, insufficient understanding of underlying ecological processes and poorly developed and competing conceptual frameworks.

2. It is suggested that final ecosystem services, such as yield, can be partitioned into components describing contributions from ecosystems (regulating and maintenance ES as natural inputs) and human inputs. This conceptual framework is tested by examining the relative importance of farming system (conventional vs. organic, indicating human inputs, and management), landscape (field shape and landscape heterogeneity), and biological control of aphids by natural enemies (indicating a regulating ES) for barley yield on 10 fields in central Sweden.

3. Although biological control was related to increased yield, its contribution was relatively small (<20%). The farming system explained most of the magnitude and variation in yield (47% of the variation, of which 34% was unique). Landscape and biological control had the largest shared contribution to variation in yield (14%). Conventional farming management seemed to have a larger effect on yield than biological control. This could be interpreted as indicating that agricultural production should be further intensified to increase yields, but a high dependency on external inputs may cause further environmental problems, such as eutrophication, and may not be sustainable.

4. Although preliminary, the results suggest that partitioning of natural and human inputs is useful to analyse the contribution of regulating ES to final ecosystem services, and how ES are co-produced by ecosystems and humans.

Key words. Additive partitioning, agricultural landscapes, aphids, biological pest control, co-production, ecosystem services, natural enemies, organic farming, variance partitioning, yield.

Introduction

Ecosystem services (ES) are the benefits that humans derive from ecosystems (Daily, 1997; MA (Millennium Ecosystem Assessment), 2005; UKNEA, 2011), and have rapidly become part of policies on biodiversity and sustainability. Some recent examples are the mapping, assessing, and valuation work initiated by the EU (MAES; Maes et al., 2014), in the UK (UKNEA, 2011), Spain (Santos-Martin et al., 2014), Sweden (Swedish EPA, 2012), as well as globally (TEEB, 2010; IPBES, 2014). The ES concept was originally intended to highlight the importance of ecosystems and the ecological processes therein for human society and welfare (Daily, 1997), and its entry in policy is both welcome and worrying. Welcome because it should, in the best of all worlds, bring the importance of benefits derived from ecosystems to society into planning and decision-making. But also worrying because the usefulness of the concept is hampered by a combination of insufficient scientific understanding of many of the underlying ecological processes generating ES (Bommarco et al., 2013; Firbank et al., 2013; Birkhofer et al., 2015; Naeem et al., 2015) and poorly developed and competing conceptual frameworks (MA (Millennium Ecosystem Assessment), 2005; Boyd & Banzhaf, 2007; UKNEA, 2011; CICES, Haines-Young & Potschin, 2013; Spangenberg et al., 2014). In addition, there are also substantial risks of economisation and commodification of nature associated with the hijacking of the ES concept by economists and policymakers who emphasise monetary valuation of ES (see
cesses is required to manage ES (Kremen, 2005; Bommarco, 2010; Gomez-Baggethun & Pérez, 2011; Lele et al., 2013; Gowdy & Baveye, 2014; Turnhout et al., 2013, 2014; but also Ahson & Hanspach, 2013; Costanza et al., 2014, and many other papers for counterarguments).

Food production and sustainable agriculture depends on a number of ecosystem services, but also to a large extent on human management and intervention (UKNEA, 2011; Lele et al., 2013; Rist et al., 2014; Spangenberg et al., 2014). An important ES in agriculture as well as many other production ecosystems is biological control of pests by natural enemies (Oerke, 2006; UKNEA, 2011), which contributes substantially to crop production worldwide (Hill & Greathead, 2000; Oerke, 2006), and also to forest production (Pimentel et al., 1997). In addition, biological pest control has been developed in greenhouses, which are intensively managed with large human inputs (van Lenteren & Woets, 1988; Messelink et al., 2013). The economic value of such biological control to society is substantial (Fleschner, 1959; Naylor & Ehrlich, 1997; Pimentel et al., 1997). However, surprisingly few studies have actually estimated the value of pest biological control for farmers (Östman et al., 2003; see below), and understanding how to manage the local and regional processes and complex food web interactions that lie behind this important service is lagging behind, despite decades of research on, e.g., control of aphid pests in intensive agriculture (e.g. Thomas et al., 1991; Ekborn et al., 1992; Bommarco, 1999; Östman et al., 2001; Thies et al., 2005).

A potential problem in ecosystem services research and policy, that risks affecting its usefulness for managing ecosystems, is that emphasis is often placed on valuation of final products, i.e. the provisioning ES that can be estimated and valued relatively easy on, e.g., the market, or by other valuation methods (e.g. Boyd & Banzhaf, 2007; Gomez-Baggethun et al., 2010; UKNEA, 2011). When valuing ES and elaborating policy for their management, such a narrow focus may result in a separation of the final ES and the processes underlying them, i.e. the intermediate regulating and maintenance ES (using the terminology of MAES, Maes et al., 2014; see Table 1). For example, if in agriculture food production (or any other final/provisioning ES) is treated as the ecosystem service to target and value, this risks de-emphasising how it is produced, the ecological processes behind food production, and the negative impacts of food production on the environment [a risk I have personally observed in both the MAES (2014) and Swedish Government and EPA processes (2011–2014) on assessment and valuation of ES]. This occurs despite the facts that the ecosystem service concept was originally intended to emphasise ecological processes (e.g. Daily, 1997) and that understanding of those processes is required to manage ES (Kremen, 2005; Bommarco et al., 2013; Birkhofer et al., 2015). Mapping and assessment exercises, e.g. Maes et al. (2014), do not easily lend themselves to understanding of underlying processes, because they do not (at present) address linkages and trade-offs between mappable ES and the underlying ecological processes. For the ecosystem services concept to be more useful in managing ecosystems, the ecological and societal processes underlying ES need to be understood both conceptually and in practice (Lele et al., 2013; Spangenberg et al., 2014). Furthermore, it is well established that this analysis should not be performed within the straitjacket framework of monetary valuation of final ES, although still some kind of socio-economic valuation may be important for planning and management decisions (e.g. Kremen & Corbera, 2010; Gomez-Baggethun & Pérez, 2011; Turnhout et al., 2013; Gowdy & Baveye, 2014).

However, the fact that natural and societal processes are jointly producing ES (Lele et al., 2013; Spangenberg et al., 2014) has seldomly been addressed, although is obvious (but implicit) in the Millennium Ecosystem Assessment (MA (Millennium Ecosystem Assessment), 2005) and UKNEA (2011). In the latter, there is in fact a table with ecosystem processes and services inputs to goods/benefits which explicitly (but almost invisibly) includes ‘other capital inputs’ to ecosystem goods (Fig. 10 in UKNEA, 2011). However, this simple but important change in the way ES are viewed and conceptualised is not formalised very well, not in the UKNEA nor anywhere else. In personal discussions with colleagues, they often argue that ES are ‘co-produced’ by ecosystems and society, but this notion of ‘co-production’ has been rather vague, and not been made operational for application to real production systems. We need methods that can examine the importance of ecosystem processes and human inputs for ES, especially their joint contributions and interactions (see Table 1 for definitions). In ecology and other disciplines, such methods are currently being used and developed, for example, variance partitioning (Cottenie, 2005), additive diversity partitioning (Anderson et al., 2011), and commonality analysis (Ray-Mukherjee et al., 2014).

The aim of this paper was to examine the unique, joint, and relative contributions of ecological processes (classically regarded as regulating and maintenance ES; MAES, 2014) and human inputs to final ES, using biological control of arthropod pests in agricultural landscapes and its effect on crop yield as a model system. It is my contention that by explicitly incorporating human inputs in the ES framework, some of the confusion regarding ecosystems services and the role of ecological processes in the production of ES can be clarified. Partly as a response to the stimulating paper by Lele et al. (2013), I suggest how their notion that ES are co-produced by ecosystem processes, human capital, and labour can be formalised. The paper also addresses how anthropogenic inputs and interventions can be analysed to enhance ES management, as called for by Bommarco et al. (2013) and Birkhofer et al. (2015). Finally, it provides an alternative framework to the ‘cascade model’ of Potschin and Haines-Young (2011) and Spangenberg et al. (2014) who also deal with the co-production of ES by society and nature.

**Conceptual framework**

For simplicity, expanding the framework of UKNEA (Mace & Bateman, 2011), assume that there are two major sets of underlying processes producing a final ecosystem service (goods, benefit or provisioning service, depending on choice of terminology). One set consists of the ecological processes that are carried out by organisms and derived from natural capital, and
another set consists of the human inputs derived from ready-to-use land (e.g. Bommarco et al., 2013). Hence, we can contrast three different production systems based on human inputs, for example, nutrient inputs from N-fertilising plants, domestic animal manure and inorganic nutrients, soil preparation, herbicides and pesticides, and harvesting by machinery. Still, natural ecological processes (regulating and maintaining ES) like nutrient cycling, biological control, pollination, and human inputs that enhance yield. Natural inputs (inputs from nature) are the soils, which contribute to increased production, but rather, the addition of nutrients (human input) supports a higher rate of plant growth processes leading to larger biomass production, i.e. there is a joint contribution of the basic plant growth processes and the input of nutrients. Some inputs may instead have negative effects, especially in a longer time perspective; for example, continuous landscape-wide use of pesticides may result in lower natural biological control potential (Geiger et al., 2010), because pesticides may reduce natural enemies, leading to decreased biological control if pesticide resistance in pests develops (as for Bt-susceptible pests; Tabashnik et al., 2013), and in the end lower yield. Hence, it is questionable if such practices are sustainable in the long term (e.g. SCAR, 2011).

Production systems such as agriculture primarily provide provisioning services, such as food and fibre. They depend on regulating and maintenance ES to varying degrees, but anthropogenic inputs (e.g. fossil fuel, nutrients, and pesticides) are often important for their function and outputs (Anderies et al., 2004; Lele et al., 2013; Rist et al., 2014), especially in intensively managed systems. In many production systems, ecosystem services have been replaced or augmented by human inputs – labour and human-made capital in the form of technology, agrochemicals, and fossil fuel energy (Rist et al., 2014; cf. Bommarco et al., 2013). However, the degree to which this has occurred varies substantially between different production systems, being lower in systems such as forestry, fisheries, and hunting, where products largely produced naturally are harvested. Human inputs are higher in agriculture and especially greenhouse production. These systems are intensively managed and actively kept from reverting into natural ecosystems (cf. fig. 1 in Rist et al., 2014).

Hence, we can contrast three different production systems that vary in the degree of human inputs (Fig. 1). In many forests, the production of tree biomass for timber or pulp is a major provisioning ES. Insect outbreaks are mainly prevented through biological control by naturally occurring predators (e.g. Ludwig et al., 1978). The main human inputs to these production systems occur during harvesting, as forest regeneration and growth until harvesting time can occur without much human intervention, and naturally occurring predators are not managed by humans. Hence, the final ES from this system are mainly produced by natural processes, with human inputs playing a minor role (Fig. 1a). In my view, this situation hardly qualifies as co-production of ES, only in the sense that human utility is necessary for ES to be obtained from a largely unmanaged system.

In agriculture, yields are much more dependent on human inputs, for example, nutrient inputs from N-fertilising plants, domestic animal manure and inorganic nutrients, soil preparation, herbicides and pesticides, and harvesting by machinery. Still, natural ecological processes (regulating and maintenance ES) like nutrient cycling, biological control, pollination, and plant biomass growth contribute, often substantially, to the final harvested yield (Daly, 1997; Pimentel et al., 1997; Östman et al., 2003; Kremen & Chaplin-Kramer, 2007; Bommarco et al., 2013). As many of these ES require human intervention to be effective, for example, by providing non-arable habitats of good quality for pollinators and natural enemies, there is a larger scope for co-production (joint contribution) among these agricultural ES. Hence both human inputs and natural processes play a large role for the final ES yield, and, in addition, there is a large joint contribution from the human and natural inputs (Fig. 1b).

Finally, consider a greenhouse system for, e.g. cucumber or pepper production, or an even more extreme hydroponic...
Fig. 1. Conceptual framework for analysing the contributions of supporting ecosystem services and human inputs to final ecosystem services (provisioning ES, goods). Final ES are the joint result of natural processes (green left circles) and human (capital) inputs (black right circles), which may contribute together, indicated by the shared segments. In forestry (a), natural processes (ecosystem services) are likely most important for final ES, whereas the dependence on human inputs increases through agriculture (b) to greenhouse horticulture (c) (see text). The size of the circles suggest relative importance in each system, but do not indicate any magnitude of yields, products or values.

system. Here, most natural processes have been replaced by human inputs. Even when biological control is used, the system is created and augmented by human inputs. This also holds when bumblebee pollination is needed for sufficient yields. Hence, the contribution of natural processes (regulating and maintenance ES) may be small but human inputs are large. There is possibly also a non-negligible joint contribution for a number of greenhouse crops (Fig. 1c).

The analysis of total output in Fig. 1 can be made in a number of ways. Similar to variance partitioning of community composition into environmental and spatial components (e.g. Cottenie, 2005; Viketoft, 2012), we can analyse the variation among sites (fields and farms) and divide it into variation emerging from different explanatory factors, such as a farming system, landscape, and natural enemies, i.e. variance partitioning of yield. This also makes it possible to decompose variation into unique and common (joint or shared) effects of different predictors. Interactions between independent variables are modelled as additional predictors. Hence the term ‘joint contribution’ is used in the following, rather than ‘interaction’. Kraha et al. (2012) discuss different methods for interpreting multiple regression analyses, such as all possible subsets regression and commonality analysis (Ray-Mukherjee et al., 2014). We can also divide total output (in this case, yield) into parts that together add up to the final product, i.e. additive partitioning of yield into its components similar to partitioning of diversity into alpha and beta components (Anderson et al., 2011 provide a recent overview).
Biological control as an ES – what do we know?

The regional or national value of biological control of pests in agriculture was recognised already at the onset of agricultural intensification in the 1950s and 1960s, and repeatedly since then (e.g. Fleschner, 1959; Naylor & Ehrlich, 1997; Pimentel et al., 1997; Hill & Greathead, 2000; Losey & Vaughn, 2006). The actual suppression of pests such as aphids by natural enemies has been more elusive, but has been experimentally demonstrated a number of times in different systems (Thies & Tscharntke, 1999; Sunderland & Samu, 2000; Östman et al., 2001, 2003; Symondson et al., 2002; Schmidt et al., 2003; Thies et al., 2005, 2011; Rusch et al., 2013). Recent reviews show that landscape complexity and natural or semi-natural habitats often increase pest control by natural enemies such as generalist insect predators, spiders, and parasitoids (Bianchi et al., 2006; Kremen & Chaplin-Kramer, 2007; Veres et al., 2013). This occurs mainly because many natural enemies rely on field edges and natural habitats such as grasslands for overwintering and reproduction (Bommarco, 1999; Landis et al., 2000; Sunderland & Samu, 2000; Collins et al., 2002; Pywell et al., 2005). There are surprisingly few studies that report the beneficial effects of natural enemies on crop yield (Bianchi et al., 2006; Kremen & Chaplin-Kramer, 2007). Östman et al. (2001, 2003) estimated from field experiments that natural enemies preying on aphids increased barley yield by around 300 kg ha$^{-1}$, corresponding to a yield increase of about 20% and a value of biological control of €41 ha$^{-1}$ in that particular year (1999). This economic value of predation on cereal aphids is of a similar magnitude as estimates by Sandhu et al. (2010; US$ 35–70).

Natural enemies are usually more abundant and diverse in organic farming systems than in conventional systems that use synthetic pesticides (Bengtsson et al., 2005; Garratt et al., 2011; Krauss et al., 2011; Tuck et al., 2014). In several cases this translated into higher pest suppression (Östman et al., 2001; Sandhu et al., 2010). Hence both farming system and landscape complexity may be important for biological control.

For efficient biological control, the predators overwintering or seeking shelter and food in natural habitats and edge zones need to disperse into arable fields and be present before pest populations start to increase (Ekborn et al., 1992). Polyphagous predators may disperse from edge zones and beetle banks at least 60–80 m into arable fields (Thomas et al., 1991; Collins et al., 2002; Holland et al., 2008). The fact that non-arable habitats are important for biological control has been used to model regionally the biological control potential from landscape variables (Jonsson et al., 2014).

Large fields have little edge (perimeter) in relation to the area. Thus, large areas of such fields may be too far away from non-arable habitats to benefit fully from the natural biological control. Hence, depending on field configuration, the need for pesticides may increase with the larger field size associated with agricultural intensification (Tscharntke et al., 2005). This is illustrated in Fig. 2, showing how the proportion of field area closer to edges than 60 m declines with an area of fields of different shapes. The mean field size in many regions in Europe is 10–20 ha (Winqvist et al., 2011; the grey line in Fig. 2). Consequently, there are good arguments for beetle banks and other measures to retain or restore field edges and natural habitats in agricultural landscapes to support biological control as well as several other ES (Watt et al., 2012). Such habitats may also increase pest abundances, but Bianchi et al. (2013) suggested that the predator support function of native vegetation may be a general phenomenon.

Partitioning agricultural yield into contributions from ecosystems and human society

I will examine the usefulness of the proposed framework, using Östman et al. (2003, data from Table 2). The study originally examined effects of the farming system (organic vs. conventional; O and C, respectively) and landscape (perimeter-to-area ratio of fields, i.e. field shape and size) on the biological control of aphids on spring barley.

The predictors in this study indicate different components in the framework. Farming system indicates differences in human inputs between conventional and organic farming, especially the use of inorganic nutrients and synthetic pesticides. There are many types of human inputs to farming that are used by both organic and conventional farmers, e.g. ploughing, sowing, harrowing, weeding, the choice of crops and crop rotations, and harvesting. The use of N-fixing crops creates a joint contribution of human management and a regulating ES. It would be appropriate to examine later the separate contributions of these different inputs, but this requires detailed knowledge of the actions of individual farmers.

Landscape may indicate different degrees of human inputs. If beetle banks and edge zones are created by farmers, they are clearly produced by human management. However, many seminatural and natural habitats, as well as edge zones to roads or water courses, are not specifically managed to enhance arable crop yield. Furthermore, in the mosaic landscape of central Sweden, many such habitats are natural features in the landscape created by geological processes during land uplift after the last ice-age, and often quite unsuitable as arable fields. For these reasons, it is useful to distinguish these features from the inputs from farming, and for want of a better term they may be termed environmental or landscape effects.

Finally, the biological control component is an ecosystem service performed by natural enemies, in this case by feeding on aphid pests. This component has clear meaning as a regulating ES, and its shared contributions with the farming system or landscape show how it together with other components contributes to the final product yield.

Study system

The aphid Rhopalosiphum padi L. is a major pest on cereals in Sweden (Ekborn et al., 1992). In 1999, we examined aphid population growth rates on spring barley within and outside experimental barriers excluding natural enemies in one field on each of five organic and five conventional farms. Well-established relationships between the number of aphid days and yield loss, and yield estimates from farmers, made it possible to calculate the yield gains from natural enemies (see Östman et al., 2001, 2003)
Fig. 2. The proportion of field area less than 60 m from edges, benefitting fully from biological control (based on Holland et al., 2008), decreases with field size, and depends on the shape of fields. This mathematical fact suggests that for a given area, elongated fields (with higher P : A-ratio) have higher potential biological control. Dots connected by unbroken line indicates square fields, broken line 1 : 4 rectangular fields, and dotted line elongated 1 : 16 fields. Dotted vertical lines show mean (13 ha) and maximum (66 ha) field sizes in central Sweden (Winqvist et al., 2011), indicating that field shape is important for potential biological control in this area.

Table 2. Partitioning of variation in actual yield into components explained by the farming system (organic or conventional), perimeter-to-area ratio (P : A-ratio) and yield gain from natural enemies [i.e. the difference between yield with natural enemies and yield without natural enemies, determined experimentally and calculated from yield loss (YL) estimates, i.e. YL(without natural enemies) − YL(with natural enemies)]. See also Fig. 3.

| Model variable(s) | $R^2$ (model) | d.f. | $P$ (model) | Proportion unique contribution |
|-------------------|---------------|------|-------------|-----------------------------|
| A. Farming system (O/C) | 0.465 | 1.8 | 0.030 | 0.337 (A) |
| B. P : A-ratio | 0.237 | 1.8 | 0.15 | 0.0618 (B) |
| C. Yield gain from NE | 0.214 | 1.8 | 0.18 | 0.0358 (C) |
| A and B. Farming system P : A-ratio | 0.608 | 2.7 | 0.038 | 0.0301 (AB) |
| A and C. Farming system Yield gain from NE | 0.582 | 2.7 | 0.047 | 0.0331 (AC) |
| B and C. P : A-ratio Yield gain from NE | 0.301 | 2.7 | 0.28 | 0.0811 (BC) |
| Total explained (A + B + C). Farming system P : A-ratio Yield gain from NE | 0.643 | 3.6 | 0.085 | 0.0643 (ABC) |
| Unexplained variation | 0.357 | | | |

Note: In this heuristic example the model A + B + C has a $R^2 = 0.64$ and $P$-value <0.09, which makes the full model meaningful to retain. Models with low $R^2$ will provide little information and may need variable deletion and model selection to be useful. Data from Östman et al., 2003, table 2).

and references therein). The effect of the ES biological control on yield was calculated as the difference in yield with and without natural enemies. All the studied conventional farms applied inorganic nutrients and herbicides, but only two of them used insecticides in the study year. The landscape was measured as perimeter-to-area ratio, which was correlated with the proportion perennial crops and medium-scale landscape heterogeneity. However, the study is small ($N = 10$ fields) and hence precision and statistical power is low. Therefore, the following analyses are mainly heuristic.

Variation in yield decomposed into different components

Variation in yield among fields (representing different farms) was decomposed into unique and joint contributions from
farming system, landscape, and biological control by natural enemies, using a version of all possible subsets regression (Kraha et al., 2012). Calculating the contributions of the three components is simple algebra after obtaining \( R^2 \)-values from seven regression analyses, one for each of A, B, C, A + B, A + C, B + C, and A + B + C (where A = farming system, B = landscape, and C = the ES biological control, measured as yield gain from natural enemies). The results are shown in Table 2 and Fig. 3.

The main contributor to variance in barley yield was the farming system, i.e. whether fields were managed organically or ‘conventionally’. This variable explained 47% of the variation in yield, with significantly lower yield on O than C fields (Generalised linear model (GLM) analysis, \( P < 0.013 \); see also Fig. 4). The unique contribution of the farming system was 34% whereas the joint contributions with other the components were much lower (3–6% each; Fig. 3). Landscape explained 24% and biological control 21% of the variation in yield, of which only 6% and 4% were unique contributions. These two components together (jointly) contributed a larger share than their unique contributions (8% together and an additional 6% together with the farming system). In addition, the effect of natural enemies on yield (biological control) tended to be larger, both absolutely and proportionally, in less complex landscapes with low P:A-ratios (GLM analyses, \( P < 0.01 \) and \( P < 0.09 \), respectively).

These analyses suggest that although biological control does contribute to reducing aphid populations (Östman et al., 2001), it is not the most important determinant of the observed variation in yield. Rather, the analyses suggest that agricultural methods linked to conventional vs. organic farming determine most of the variation in cereal yields in this area of Sweden.

**Additive partitioning of mean yield**

Another way of analysing the importance of the regulating ES biological control versus human inputs for the final ES crop yield is to partition the mean yield into underlying components. In additive partitioning, the target variable, here yield, is composed of a set of variables starting from a ‘baseline’ level. As the P:A-ratio varied quite a lot in this study, its mean is not particularly informative. It is also, for agricultural yield, natural to begin with organic farming, which had the lowest yield, and add on effects of conventional farming methods and natural enemies, while it is not obvious how the landscape fits naturally in the addition. Therefore, the landscape effect is not considered, and only the farming system (O or C means) and the mean measures of biological control are left to contribute to the mean yield and mean potential yield.

The results are clear as regards the contribution of biological control to yield – it was quite small (Fig. 4). The mean increase in yield because of natural enemies was 303 kg ha\(^{-1}\), with no clear difference between organic and conventional fields. However, as yields were lower on O fields (compare left column of Fig. 4a vs. b), the proportional increase in yield was substantially higher in organic than conventional farming (right column of Fig. 4). On average, the contribution from human inputs, i.e. management such as soil cultivation, N fertilisation, and on conventional fields inorganic nutrient additions, herbicides and pesticides, contributed to 71–77% of the potential barley yield (80% and 88% of actual yield in O and C, respectively), whereas natural enemies contributed an additional 18% in O and 11% in C (20% of actual yield in O and 12% in C). These results suggest that organic farming indeed relies more on ecosystem services such as biological control, but that human inputs in terms of management are the main factor...
Discussion and conclusions

The results from these analyses emphasise the pivotal role of human management for agricultural yield. However, most ES in agriculture are produced jointly by human management and natural ecosystem processes, in many cases interacting with each other and other environmental factors. This suggests that ecosystem services are not simply co-produced by society and ecosystems in the sense that co-production means that human benefits of an ES have to be identified for an ES to be recognised. Rather, ecosystem services are to different degrees co-produced or jointly determined by humans and nature depending on the different contributions of human and natural inputs to final provisioning ES (goods) (cf. Rist et al., 2014). Partitioning methods like the ones discussed here seem useful to examine the relative contributions of natural and human inputs, and to highlight underlying natural processes and management actions. Such knowledge is needed for better management of ES. More detailed examinations in systems varying in human inputs are needed for a comprehensive understanding of these joint contributions and interactions (cf. Fig. 1). Also, describing ‘farming system’ with the actual factors characterising it, such as fertiliser inputs, herbicide use, and soil cultivation, and adding more ecosystem processes, e.g. pollination, would be worthwhile.

The results of both partitioning analyses suggest that on these farms management associated with conventional farming, mainly inorganic nutrient fertilisation, herbicide and pesticide use, was a major determinant of both actual and potential yield (Fig. 4c). However, how large this effect is hinges on the difference in yields between organic and conventional farming. In the present case, organic yields were < 50% of conventional, which is a rather large difference. The magnitude of yield differences between organic and conventional agriculture are debated (Badgley et al., 2007; de Ponti et al., 2012; Seufert et al., 2012) but on average organic farming yields are 75–80% of conventional (ibid). However, it is particularly low in cereals (Seufert et al., 2012) and high external input countries in NW Europe (de Ponti et al., 2012).

Will future agricultural production depend on further intensification of management rather than on ecosystem services, as might be suggested based on the present analyses (cf. sustainable intensification; Godfray et al., 2010; Garnett et al., 2013)? Not necessarily. I have only analysed a single ES, and many ES interacting with management practices were not examined. Some of these are N-fixation, nutrient cycling and decomposition, plant growth, soil organic matter maintenance, and pollination of pollination-dependent crops (Bommarco et al., 2013). Agriculture also produces other provisioning and cultural ES than crop yield (Firbank et al., 2013; Robertson et al., 2014). That aspects other than yield were not included is problematic, especially when discussing ecosystem management, because many ES are related to each other forming synergies and trade-offs among them (Raudsepp-Hearne et al., 2010; Gamfeldt et al., 2013; Lele et al., 2013; Robertson et al., 2014).

The large contribution of especially conventional management to yield could also be viewed as an indication of a high dependency on external inputs in the intensive Swedish agriculture. This may not be sustainable in the long term, because of possible future resource, energy, and water scarcities globally (e.g. Paillard et al., 2011; de Ponti et al., 2012), nor in the short term because of the large environmental impacts of intensive agriculture, such as pollution, eutrophication, declining biodiversity, climate change impact, and deteriorating ecosystem services (e.g. Krebs et al., 1999; MA (Millennium Ecosystem...
Assessment), 2005; Tscharntke et al., 2005; de Ponti et al., 2012; Bommarco et al., 2013; Robertson et al., 2014). These negative effects of agriculture also need to be accounted for when assessing how agricultural outputs to society depend on ecosystem services and human inputs. However, inclusion of ‘ecosystem disservices to humans’ and ‘human disservices to ecosystems’ into the present framework would need further conceptual elaboration in the context of human–nature interactions.

To summarise, I have utilised an established set of statistical methods in a new context to examine the joint contribution from natural (ecosystem) processes, mainly regulating and maintenance ecosystem services, and human inputs to final provisioning ES, such as agricultural yield. The methods do not directly examine the ecological processes behind the indirect and final ES, but they can be used to identify the most important ES for future process-related studies. They can also show the current balance of human vs. natural inputs in a production system, and suggest ways in which ES can support or substitute human inputs to, for example, agriculture (Bommarco et al., 2013). The analyses decomposing yield into predictor variables related to farming system management, landscape, and the ES biological control suggest that in intensively managed agricultural landscapes, human inputs are more important for yields than ecosystem services such as biological control. However, this conclusion should be treated with extreme caution, because neither the negative environmental effects nor the questionable long-term sustainability of intensive agriculture are accounted for, nor were other ES in agricultural landscapes and how these interact with management examined.

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