




RESEARCH ARTICLE

Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect effects of organic production

Ulrika Samnegård¹ | Georgina Alins² | Virginie Boreux³ | Jordi Bosch⁴ |
Daniel García⁵  | Anne-Kathrin Happe⁶ | Alexandra-Maria Klein³ |
Marcos Miñarro⁷ | Karsten Mody⁶ | Mario Porcel⁸ | Anselm Rodrigo⁴ |
Laura Roquer-Beni⁴ | Marco Tasin⁸  | Peter A. Hambäck¹ 

¹Department of Ecology, Environment and Plant Sciences, Stockholm University, Stockholm, Sweden; ²Institut de Recerca i Tecnologia Agroalimentàries, Lleida, Spain; ³Nature Conservation and Landscape Ecology, University of Freiburg, Freiburg, Germany; ⁴CREAF, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain; ⁵Unidad Mixta de Investigación en Biodiversidad (CSIC-UO-PA), Universidad de Oviedo, Oviedo, Spain; ⁶Department of Biology, Technische Universität Darmstadt, Darmstadt, Germany; ⁷Servicio Regional de Investigación y Desarrollo Agroalimentario, Asturias, Spain and ⁸Department of Plant Protection Biology, Swedish University of Agricultural Sciences, Alnarp, Sweden

Correspondence

Peter Hambäck

Email: peter.hamback@su.se**Present address**

Ulrika Samnegård, Department of Biology, Lund University, Lund, Sweden

Funding information

BiodivERSA-FACCE-JPI, Grant/Award Number: 2014-74; Svenska Forskningsrådet Formas, Grant/Award Number: 2013-934 and 2014-1784; Ministerio de Economía y Competitividad, Grant/Award Number: PCIN-2014-145-C02; German Federal Ministry of Education and Research, Grant/Award Number: 01LC1403; Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria

Handling Editor: Jennifer Firn

Abstract

1. Apple is considered the most important fruit crop in temperate areas and profitable production depends on multiple ecosystem services, including the reduction of pest damage and the provision of sufficient pollination levels. Management approaches present an inherent trade-off as each affects species differently.
2. We quantified the direct and indirect effects of management (organic vs. integrated pest management, IPM) on species richness, ecosystem services, and fruit production in 85 apple orchards in three European countries. We also quantified how habit composition influenced these effects at three spatial scales: within orchards, adjacent to orchards, and in the surrounding landscape.
3. Organic management resulted in 48% lower yield than IPM, and also that the variation between orchards was large with some organic orchards having a higher yield than the average yield of IPM orchards. The lower yield in organic orchards resulted directly from management practices, and from higher pest damage in organic orchards. These negative yield effects were partly offset by indirect positive effects from more natural enemies and higher flower visitation rates in organic orchards.
4. Two factors other than management affected species richness and ecosystem services. Higher cover of flowering plants within and adjacent to the apple trees increased flower visitation rates by pollinating insects and a higher cover of apple orchards in the landscape decreased species richness of beneficial arthropods.
5. The species richness of beneficial arthropods in orchards was uncorrelated with fruit production, suggesting that diversity can be increased without large yield

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2018 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

loss. At the same time, organic orchards had 38% higher species richness than IPM orchards, an effect that is likely due to differences in pest management.

6. *Synthesis and applications.* Our results indicate that organic management is more efficient than integrated pest management in developing environmentally friendly apple orchards with higher species richness. We also demonstrate that there is no inherent trade-off between species richness and yield. Development of more environmentally friendly means for pest control, which do not negatively affect pollination services, needs to be a priority for sustainable apple production.

KEYWORDS

apple production, biological control, integrated pest management, natural enemies, organic management, pollination services, species richness, structural equation model

1 | INTRODUCTION

Fruit consumption is an important part of human nutrition, and the second most important fruit crop globally is apple (FAO, 2018). Therefore, the sustainable production of apples is an important goal for human food provisioning. In temperate regions, the by far largest area of fruit production is apple orchards and, similar to other crops, agricultural intensification of these orchards during the last century has increased production through high input of inorganic fertilizers, pesticides, and herbicides (Reganold, Glover, Andrews, & Hinman, 2001). For instance, chemical pest control is essential for profitable apple production, as more than 50% of the crop may be lost in orchards with no control (Cross, Fountain, Marko, & Nagy, 2015). Intensification in apple orchards, however, leads to increased production costs as well as to environmental detriments both within the orchard and in surrounding areas (Reganold et al., 2001). These detrimental effects have increased the interest in developing more environmentally friendly production, through either integrated production or organic management, in which the enhancement of ecosystem services from natural enemies can partly replace the use of chemical pesticides in suppressing pest populations (Dib, Sauphanor, & Capowiez, 2016; Simon, Bouvier, Debras, & Sauphanor, 2010).

The intensification of agriculture also threatens the delivery of pollination services from the wild pollinator community (Klein, Fornoff, Mupepele, & Boreux, 2018; Potts et al., 2010). For pollinator-dependent crops such as apple, decreased pollination services result in lower seed and fruit set and in a lower profitability for the farmer (Garratt et al., 2016; Klein et al., 2018; Mallinger & Gratton, 2015). To obtain better pollination, orchard owners often use managed pollinators such as honeybees, and in some cases bumblebees. However, the efficiency of these managed pollinators is debated, and is often found to be lower than that of wild pollinators (Garratt et al., 2016; Mallinger & Gratton, 2015). The availability of managed pollinators may also vary between years

leading to a vulnerable system if managed bees are relied upon to provide the majority of the pollination services (Breeze, Bailey, Balcombe, & Potts, 2011).

Agricultural intensification affects beneficial arthropods, and their delivery of ecosystem services, not only due to local management but also through simplification of the surrounding landscape (Lichtenberg et al., 2017). The abundance of both natural enemies and pollinators is often lower in simplified landscapes, due to lower amounts of alternative resources or fewer overwintering sites (Shackelford et al., 2013), but there is also often an interaction between the local management and structure of surrounding habitats. For instance, it seems that the negative effects of intensive field management on pollinating insects are mainly observed in relatively homogeneous landscapes (Rundlöf, Nilsson, & Smith, 2008; Williams & Kremen, 2007).

In the European Union, subsidies have been available since the late 1980s to promote environmentally friendly farming systems, at both local and landscape scales (Primdahl, Peco, Schramek, Andersen, & Onate, 2003). These agri-environmental schemes, which are mainly implemented on a voluntary basis, include “environmentally favourable extensification of farming”, “integrated farm management and organic agriculture”, and “preservation of landscape and historical features such as hedgerows, ditches, and woods”. Even though subsidies have been in place for some time, their efficiency to promote biodiversity, and how they affect ecosystem services and yield in apple production systems are less clear (but see Albert, Franck, Gilles, & Plantegenest, 2017). A problem with implementing efficient management strategies is that ecosystem services are often differently affected by the same management action (Shackelford et al., 2013). Different responses for diversity-related ecosystem services to the same management action may be expected because species vary in their life history, but maximizing the total output of ecosystem services on apple production necessitates that potential trade-offs arising from management are identified and accounted for (Power, 2010).

One basic trade-off between ecosystem services and agriculture emerges when management that aims to increase crop yield by stimulating plant growth (e.g., by adding nutrients and water, or by removing competing weeds) also indirectly reduce production by affecting the ecosystem services of pest control and pollination (Power, 2010). Trade-offs also occur in management aimed to affect diversity-related services or disservices (positive and negative effects from biodiversity, respectively), when actions to promote beneficial arthropods also benefit pest species, or when actions to reduce pest species also negatively affect beneficial species (Saunders, Peisley, Rader, & Luck, 2016; Tscharntke et al., 2016). For instance, several studies suggest that flower strips, which are commonly planted to benefit pollinators and natural enemies (Lichtenberg et al., 2017; Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012), may not only affect the potential for pest control but also pest densities and crop damage (Tscharntke et al., 2016). Other studies suggest that flower strips to enhance natural enemies are most efficient when placed inside orchards (Saunders & Luck, 2018), but these strips may then compete with apple trees for nutrients and water (Granatstein & Sánchez, 2009). Similarly, pesticides may negatively affect natural enemies and pollinators, leading to reduced biocontrol (Dib et al., 2016; Fountain & Harris, 2015) and pollination services (Pisa et al., 2015; Stanley et al., 2015). Because apple production is often limited by pest damage and pollination, alternative pest control measures without negative effects on natural enemies and pollinators are preferable. Natural enemies and pollinators are generally promoted by retaining sheltering habitats within or next to the production areas or by providing nectar and pollen resources in the form of planted or conserved flowering plants present in alleyways, margins, and hedgerows (Campbell, Wilby, Sutton, & Wackers, 2017; Miñarro & Prida, 2013).

In this study, we examined trade-offs between production and ecosystem services, and between ecosystem services and disservices, by comparing integrated pest management (IPM) and organic apple production, as a broad classification of management systems. We evaluated the role of management (organic vs. IPM) in a study design accounting for agri-environmental structures and landscape composition affecting diversity at three spatial scales: within orchards, adjacent to orchards, and in the surrounding landscape. The variables include both floral resources for pollinators and overwintering sites for all arthropods, estimated through the cover of flowering plants and the area of agri-environmental structures within and close to the orchard, and the amounts of bee-friendly habitats in a larger area around the orchard, which may increase the species pool for the local orchard. We also included the cover of orchard area around each focal orchard, as a measure of the homogenization of the landscape. The study was performed in 85 apple orchards in three European countries (Spain, Germany, and Sweden) to cover regional variation in apple production. We collected data on flower visitation rates, pollination deficits, natural enemies, pests and fruit production, and used a structural equation model to disentangle the direct and indirect effects of management and environmental variables on seed set and fruit production.

2 | MATERIALS AND METHODS

2.1 | Study regions

The study included three important apple-growing regions; north-eastern Spain (SP), southern Germany (GE), and southernmost Sweden (SW) (Figure 1). In Spain, we selected apple orchards located in the provinces of Lleida and Girona, Catalonia. In Germany, we selected apple orchards in the lake Constance region, Baden-Württemberg. In Sweden, we selected apple orchards on the east and west coasts of the county Skåne. The target apple varieties in the study orchards were common for each region: Gala and Golden Delicious in Spain, Braeburn in Germany, and Aroma and the sub-variety Amorosa (but included some Ingrid Marie and Rubinola) in Sweden.

Within each region, we selected 28 (SP and SW) or 30 (GE) orchards, half of which were managed organically and the other half were managed according to IPM guidelines (Malavolta & Cross, 2009). One Swedish orchard was excluded before analysis because it had been abandoned. The orchards were selected along a land-use gradient, using forest cover as a proxy, with approximately half the orchards harbouring agri-environmental structures (e.g., hedgerows, flower strips, margins with ruderal vegetation) in their close surroundings (up to 20 m from the edge of the trees). IPM orchards were managed with a similar crop protection strategy and with foliar and mineral fertilizers applied at multiple times along the season. Crop protection in these orchards involved a range of chemicals for pest, weed, and disease control, but the specific active ingredient differed somewhat between countries and orchards. Among the organic orchards, the majority were certified in accordance with European or National legislation (Council Regulation (EC) No 834/2007), which involves more restrictive crop protection strategies and organic fertilizers. In these orchards, pest control mainly occurred through use of natural extracts (neem, pyrethrum), micro-organisms (*Bacillus*

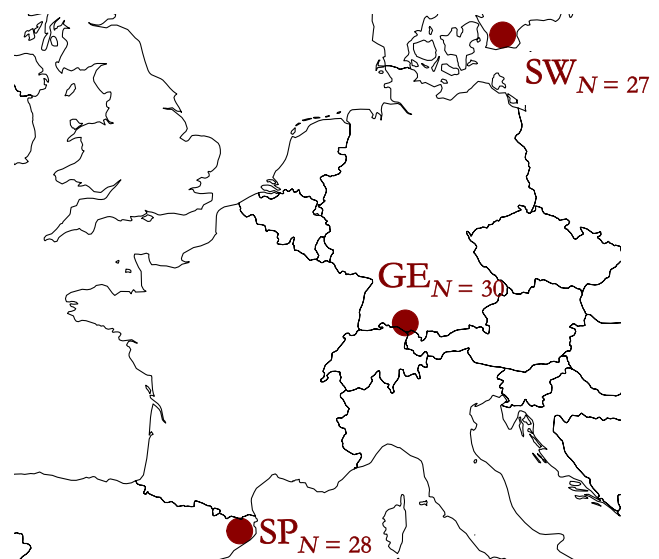


FIGURE 1 Map showing the study areas in Sweden (SW), Germany (GE), and Spain (SP)

thuringiensis), viruses (e.g., granulosus virus vs. codling moth), and through mating disruption of specific insect pests, while fungal control strategies involve compounds such as sulphur and lime sulphur. Thus, the contrast of IPM versus organic management involves differences not only in the intensity and type of chemicals for pest control but also in the input and availability of nutrients for crop plants (expectedly higher in IPM than in organic), due to the use of chemical fertilizers and chemical weed control (de Ponti, Rijk, & van Ittersum, 2012). A few uncertified orchards in Sweden and Spain were managed as under organic guidelines with no chemical inputs, and these orchards were considered organic in this study.

2.2 | Field sampling

Within orchards, we quantified natural enemies, pollinators, pollination success, pests/pest damage, and fruit production. Fieldwork was performed during 2015, and data collection was adjusted to the annual cycle of apple production in each region. Pollination was studied during flowering and pest incidence and damage were surveyed at relevant pest phenological stages. Due to climate differences, the timing of data collection varied between the three countries. We estimated natural enemy abundance by beating one apple branch of a representative size on 24 trees per orchard once within 2 weeks after apple flowering, and all collected natural enemies were identified to species or morphospecies. Trees used for beating samples were randomly selected in one 40 m transect per orchard, along a single row perpendicular to the orchard border (SP and SW) or two rows (GE). Natural enemy abundance was calculated as the total number of natural enemy individuals collected per transect, and the richness as the total number of natural enemy species per transect. In natural enemies, we included spiders, predatory coleopterans (mainly Cantharidae and Coccinellidae), earwigs, predatory heteropterans (mainly Anthocoridae), predatory dipterans (mainly Hybotidae, Empididae, and Dolichopodidae), lacewings, and harvestmen.

The visitation rate and richness of apple flower-visiting wild pollinators was estimated once per orchard from transect walks during apple flowering, in one transect close to the orchard border (0–20 m), and one transect in the orchard interior (20–40 m from border). Each walk lasted 5 min and was repeated three times throughout the day (total 30 min sampling per orchard). Visitation rates were calculated as the number of observed pollinator visits per 1,000 flowers per 5 min. We recorded all pollinators visiting apple flowers, and collected species for identification in the laboratory. We only included wild bee and syrphid fly species in the estimate of flower visitation rates as other groups (e.g., beetles) are unlikely pollinators of apple (Kendall, 1973; Ramirez & Davenport, 2013). We pooled the species number of flower visitors and natural enemies to obtain an estimate of the total number of beneficial arthropod species per orchard (hereafter, beneficial species richness). To estimate pollination services, we performed a hand pollination experiment on three trees per orchard, where each tree had one branch dedicated to open and one to supplementary pollination

treatments. For hand pollination, we used pollen from pollinizer trees growing within or adjacent to the orchard. Using these data, we estimated the pollination deficit as (seed set of supplementary pollinated flowers) – (seed set of open-pollinated flowers) for fruit-lets in May–June. A positive value implies a pollination deficit, indicating insufficient pollination services. As an estimate of apple production, we calculated an index based on the fruit set, proportion damaged fruits, and mean apple weight calculated for apples collected on three marked branches on five trees per orchard. The production index equals the weight of undamaged fruit per 100 flowers, and was calculated as (the proportion of undamaged apples at harvest) × (mean weight of harvested apples) × (fruit set). Fruit set is the per cent flowers that produced fruits at harvest from 18 branches per orchard, the proportion of undamaged fruits equals one minus damage (see next paragraph), and mean weight was calculated from up to 18 apples per orchard.

We estimated pest densities and damage in two ways representing the main pest problems for orchard owners. First, we estimated aphid abundance by counting the proportion of branches infested by aphid colonies, for each aphid species separately on 13–60 trees per orchard. The main aphid pests in all study orchards and in apple orchard across Europe are rosy apple aphid (*Dysaphis plantaginea* [Passerini], hereafter RAA) and woolly apple aphid (*Eriosoma lanigerum* [Hausmann]) (Blommers, 1994). RAA was by far the most abundant species, particularly in Sweden and Spain, and is often considered as the most damaging aphid, so we only considered this species. Second, we estimated fruit damage from other pest species for 24 apples on 37 trees per orchard (888 fruits per orchard), in the same transects as the pollination study, at the time of harvest, and used these data to calculate the proportion of damaged apples. This measure reflects the damage of codling moth (*Cydia pomonella* L.), sawflies, geometrids, and leaf rollers. The specific pests inflicting the damage differed between countries, with leaf rollers and winter moth (*Operophtera brumata* L.) doing most damage in the Swedish orchards, leaf rollers (Tortricidae), and sawflies (*Hoplocampa testudinea* Klug) in German orchards and codling moth in Spanish orchards. These estimates do not cover damage that cause fruit drop before harvest, but such loss would be reflected in the fruit set and thus in the apple production variable.

2.3 | Estimating environmental variables

To understand the effect of local conditions, we estimated flowering plant cover and the area covered by agri-environmental structures (AES) within and in the close surroundings of each orchard. First, we estimated the cover of flowering plants once per orchard as the per cent cover of plants attractive to pollinators (hereafter flower cover) near the time of apple flowering. Flowering plants include those species flowering at any time during the year and not only at the time of the survey, to assess the total amount of resources available for pollinators. To identify plant species attractive to pollinators, we used the BioFlor Database (Kühn, Durka, & Klotz, 2004). Flower cover was estimated for each species from six 1 × 1 m² plots between

apple rows and from six plots outside the apple rows and summed across species. Second, we estimated the total surface cover of AES in m² within 20 m of the transects. AES include hedgerows (including edges with old trees and tree rows), forest edges, forests (river forests, tree plantations), fallow lands (including abandoned fields), semi-natural grasslands (terraced field margins, embankments), and orchard meadows.

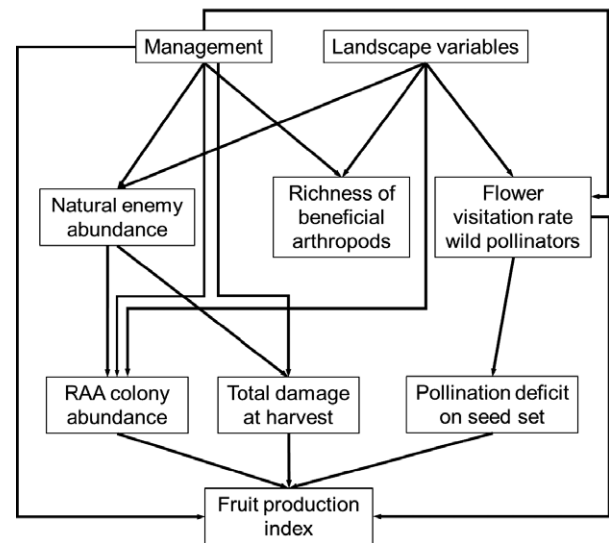
To understand landscape effects, we estimated the proportion of bee-friendly habitat for each orchard within 1 km from the transect centre. We defined bee-friendly habitats for each country based on expert knowledge, including shrubland, dry land orchards, and abandoned orchards in Spain, orchard meadows in Germany, and semi-natural grasslands in Sweden. We estimated the cover of apple orchards as the proportion of surface area covered by this crop within 1 km from the transect, as a proxy for homogeneous landscape composition and land-use intensity in our apple production regions. To quantify landscape characteristics, we used official digital maps for Spain and Germany (Carreras & Diego, 2009; LGL 2016; SIOSE 2015), spatially explicit data on land use from the Swedish Board of Agriculture (Integrated Administrative Control System, IACS) and Geographic Information Systems and Remote Sensing software ArcView 10.3.1 and MiraMon.

2.4 | Statistical analyses

To assess the direct and indirect effects of management, local orchard conditions, adjacent site conditions, and landscape composition across orchards, we developed a structural equation model (SEM) with fruit production as the endpoint variable. As intermediary variables, we used the total species richness of beneficial arthropods (flower visitors and natural enemies), natural enemy abundance, flower visitation rate by wild pollinators, RAA abundance, pest damage at harvest, and pollination deficit. To build the SEM, we combined seven mixed effects models (lme in the R package *nlme*) in a piecewise SEM (Lefcheck, 2016), with country as random effect. To reduce the number of variables, we first evaluated each individual lme and removed non-significant variables describing agri-environmental or landscape composition. Following this, we evaluated each lme by plotting standardized residual against fitted values and predictor variables. For pest damage, residual plots indicated heteroscedasticity between management and between countries. We therefore modelled variance in this submodel using the *VarIdent* option. For apple production and flower visitation rate, residual plots indicated a loglinear relationship with predictive variables and these variables were log₁₀-transformed before inclusion in the final model.

We assessed the initial SEM (Figure 2a) by the D-separation test to detect missing paths and tested the overall model with Fisher's C statistics. We added significant missing paths and removed non-significant paths until the AIC was no longer reduced. We accounted for two correlated errors; between species richness and natural enemy abundance, and between RAA abundance and total damage at harvest. When presenting the final SEM, we compared the relative importance of pathways using standardized path coefficients.

(a) Initial SEM model



(b) Final SEM model

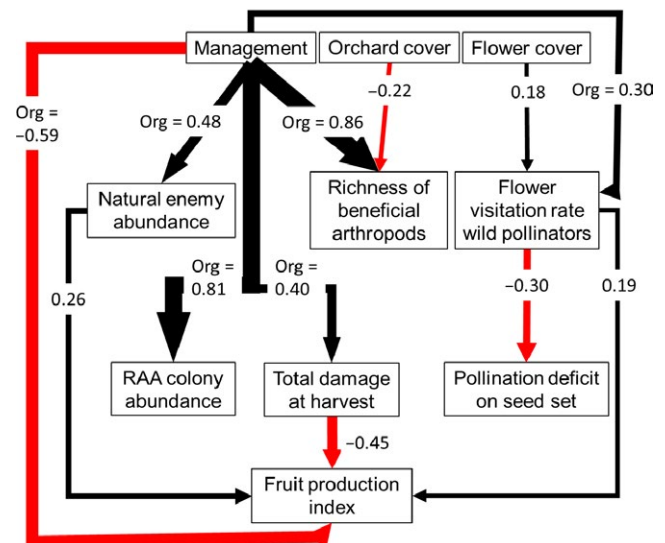


FIGURE 2 (a) Initial and (b) final structural equation model (SEM) showing significant direct and indirect paths from management, orchard landscape cover and flower cover. The landscape variables tested in the initial SEM were flower cover, AES cover, orchard cover, and cover of bee-friendly habitats. Arrow thickness in the final SEM is proportional to the standardized path coefficients (figures next to the paths). The colour of the path indicates the sign of the effect (red = negative, black = positive). The sign connected to management type refer to organic management relative to IPM. The model includes correlated errors between natural enemy abundance and richness of beneficial insects ($p < 0.0001$), and between (rosy apple aphid) RAA abundance and total damage at harvest ($p < 0.0001$) but these arrows are omitted in the figure

To assess the generality of the model across countries, we ran the final SEM for each country separately as a post hoc comparison. This step should be viewed cautiously as the model is applied on smaller datasets, but it serves the purpose of indicating if patterns in the SEM are mainly caused by patterns in one country. In this comparison, we present unstandardized parameter values because these

provide a better comparison between countries. To assess the relationship between apple production and species richness, we related these variables following the removal of partial effects from other variables in the lme-models using the `remef` command (Hohenstein & Kliegl, 2015).

3 | RESULTS

When analysing the combined direct and indirect effects of management on fruit production, we found that organic orchards on average had a 48% lower fruit production compared to IPM orchards ($F_{1,76} = 20.9, p < 0.0001$) and this effect size did not vary between countries ($F_{2,76} = 2.1, p > 0.13$). However, the variation for each category was large and the production of the most productive organic orchards exceeded the mean of IPM orchards (Figure 3). The initial SEM showed a good fit (Fisher's $C = 69.4, df = 60, p = 0.18$), but the D-separation test indicated a missing direct path from the natural enemy abundance to apple production (for data used in SEM see Samnegård et al., 2019). Adding this path increased the fit of the SEM (Fisher's $C = 47.9, df = 56, p = 0.54$), and did not change the model otherwise (Figure 2b). In the final SEM, management had a strong direct effect, and several indirect effects, on apple production with lower production for organic orchards. Both natural enemy abundance and flower visitation rates were higher in organic orchards, creating indirect positive effects from organic management on apple production (Figure 2b). Fruit damage at harvest was higher in organic orchards, creating an indirect negative effect from organic management on apple production (Figure 2b). It is also notable that effects from the area of AES and bee-friendly habitats

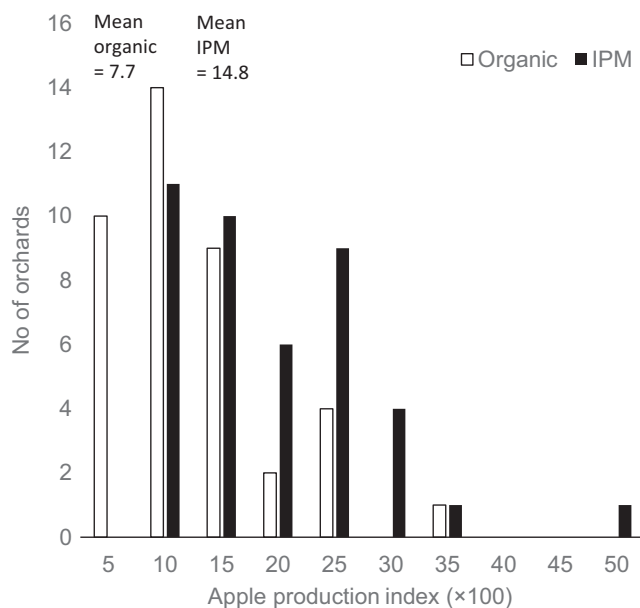


FIGURE 3 Distribution of the fruit production index for organic orchards and IPM orchards. For illustrative purposes, the index is corrected for differences between countries by multiplying the value of each orchard by the ratio of the overall and country means

were non-significant and were excluded already in the initial model. The only effects from the agri-environmental or landscape structures that were retained in the final SEM were positive effects of flower cover on wild pollinator visitation rates and negative effects of orchard cover on species richness of beneficial arthropods (Figure 2b).

When comparing parameter values between countries and with the final SEM (Table 1), differences were relatively small. In three cases, parameter values for the three countries deviated based on the difference of parameter values and the magnitude of the SE . First, estimated parameter values for the relationship between natural enemy abundance and fruit production was lower for Sweden and did not overlap with the estimates for other countries. Second, estimated values for the relationship between management and fruit damage were higher for Sweden and Spain compared to Germany. Finally, estimated parameter values for the relationship between management and aphid abundance (mainly RAA) were lower for Germany than for other countries.

When assessing the relationship between fruit production and beneficial arthropod species richness, while partialling out the effect of orchard cover in the surrounding landscape, we found no relationship between fruit production and species richness (Figure 4). This pattern was true for both organic and IPM orchards, but there was an effect of management where organic orchards had on average 38% more species for the same production of apples (13.0 vs. 9.4 species).

4 | DISCUSSION

Management differences between organic and IPM in apple orchards evidently had strong effects on fruit production, pest damage, beneficial arthropod species richness, and diversity-related ecosystem services. On average, fruit production was 48% lower in organic orchards, which is a larger difference than between organic and conventional management in other crops (Seufert, Ramankutty, & Foley, 2012). Importantly, the overall effect on fruit production was due to a combination of direct management effects and indirect effects due to higher pest damage in organic orchards. Pest control strategies in organic orchards are typically less effective than in orchards that use synthetic pesticides, and the commercial output of apple production is sensitive to damage, as damaged fruits cannot be sold as high-quality apples for direct consumption on the market. The unidentified direct effects may be related to differences in fertilizer and water/irrigation use (Berry et al., 2002; Klein, Hendrix, Clough, Scofield, & Kremen, 2015), as well as fungal disease control and weed management, which were not accounted for in our study. While pest damages were lower in IPM orchards, organic orchards were more strongly benefitting from diversity-related ecosystem services, as these orchards had both a higher abundance of natural enemies and a higher flower visitation rate from wild pollinators, increasing fruit

TABLE 1 Unstandardized path coefficients (mean \pm SE) of the final model using the whole dataset, with country as random effect, and the three datasets separately. For management, coefficients indicate differences of organic management to IPM

Response	Predictor	Total	SP	GE	SW
Fruit production	Management	-0.19 ± 0.07 ($p < 0.005$)	-0.064 ± 0.11	-0.23 ± 0.14	-0.12 ± 0.15
-	Fruit damage	-1.72 ± 0.40 ($p < 0.004$)	-1.83 ± 0.51	-1.84 ± 3.12	-2.87 ± 0.95
-	NE abundance	0.0062 ± 0.0022 ($p < 0.007$)	0.0082 ± 0.0050	0.0064 ± 0.0059	0.0009 ± 0.0036
-	Flower visitation	0.057 ± 0.028 ($p < 0.05$)	0.046 ± 0.063	0.004 ± 0.078	0.096 ± 0.075
Pollination deficit	Flower visitation	-0.77 ± 0.31 ($p < 0.03$)	-1.49 ± 0.45	-0.33 ± 0.65	-0.07 ± 0.51
Flower visitation	Flower cover	0.0075 ± 0.0034 ($p < 0.03$)	0.013 ± 0.005	0.0057 ± 0.0058	-0.0028 ± 0.009
-	Management	0.33 ± 0.17 ($p < 0.05$)	0.32 ± 0.25	0.048 ± 0.33	0.69 ± 0.26
Fruit damage	Management	0.034 ± 0.009 ($p < 0.0003$)	0.11 ± 0.04	0.025 ± 0.008	0.12 ± 0.02
RAA abundance	Management	0.26 ± 0.05 ($p < 0.0001$)	0.36 ± 0.11	-0.011 ± 0.009	0.46 ± 0.10
Richness of beneficials	Management	4.10 ± 0.78 ($p < 0.0001$)	5.36 ± 1.32	3.51 ± 0.97	3.18 ± 1.73
-	Orchard cover	-0.046 ± 0.019 ($p < 0.02$)	-0.023 ± 0.021	-0.12 ± 0.03	-0.037 ± 0.070
NE abundance	Management	6.49 ± 2.46 ($p < 0.02$)	8.86 ± 3.64	7.00 ± 4.67	3.48 ± 4.35

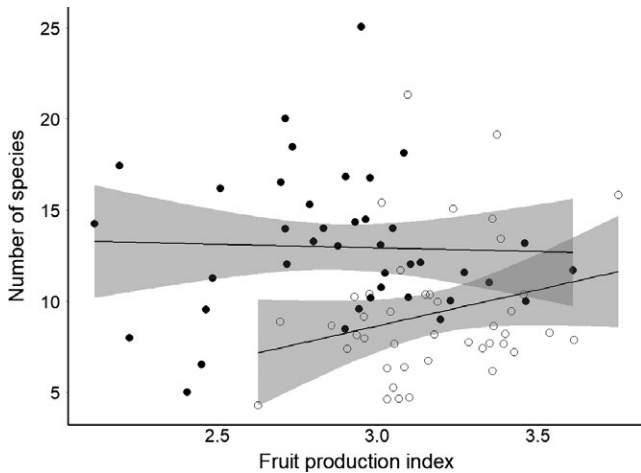


FIGURE 4 Partial residuals, prediction lines, and confidence bands between species richness of beneficial arthropods and the fruit production index (log₁₀-transformed), for organic (●) and IPM (○) orchards

production. While these indirect positive effects were not strong enough to overcome the negative effects of organic management on fruit production, the pattern suggests that methods to increase natural enemy abundance and wild pollinator visitation have the potential to reduce the yield gap between organic and IPM orchards. This conclusion is supported by the fact that some organic orchards had a fruit production that was well above the mean production of IPM orchards (Figure 3).

A concern for agricultural systems in general has been that increased production often causes a reduction in biodiversity, and that efforts to reduce these negative effects entail a cost in terms of reduced production (Clough et al., 2011; Gabriel, Sait, Kunin, & Benton, 2013). Our study does not support this concern for apple orchards. Species richness of beneficial arthropods and apple production in our study were largely uncorrelated (Figure 4), and this

pattern was similar in both organic and IPM orchards. If anything, there was a close to significant positive relationship between apple production and species richness for IPM orchards. Clough et al. (2011) similarly found no trade-off between crop yield and biodiversity in smallholder cacao production systems, suggesting that productivity costs related to the maintenance of a high biodiversity may be small for some systems. On the other hand, organic orchards in our study had on average 38% more beneficial species for similar levels of apple production, confirming the previous conclusion that organic management supports a higher local species richness of arthropods (Rusch, Birkhofer, Bommarco, Smith, & Ekbom, 2014). We can only speculate on the main causes of this difference, but it seems plausible that it is mainly due to differences in pest control methods that affect survival of non-target organisms (cf., Lefebvre et al., 2017; Park, Blitzer, Gibbs, Losey, & Danforth, 2015) or differences in weed management effects on species diversity within the orchards (Gurr, Wratten, & Luna, 2003).

The effect of orchard management on arthropod richness often interacts with habitat composition at the local and landscape levels, where intensification and homogenization at the landscape level result in decreased arthropod richness in otherwise species-rich habitats (Landis, 2017). The use of various AES for conservation has long been promoted in the European Union (Primdahl et al., 2003), but the effectiveness of these measures has been questioned (Batáry, Dicks, Kleijn, & Sutherland, 2015; Tschamntke et al., 2016). In our study, we found that a higher cover of apple orchards in the surrounding landscape reduced species richness of beneficial arthropods within the orchard. A relatively uniform landscape with apple orchards may be less favourable for biodiversity than a more heterogeneous landscape, because most apple orchards in any landscape are managed according to IPM (see also Joshi, Otieno, Rajotte, Fleischer, & Biddinger, 2016; Marini, Quaranta, Fontana, Biesmeijer, & Bommarco, 2012). On the other hand, we

did not find a direct effect of AES surface on either species richness of beneficial arthropods, natural enemy abundance, and fruit production. However, it is premature to argue that AES are not useful in apple orchards since only a few orchards in our study had actively established these structures. Our measures mainly reflect the natural occurrence of these habitat types in the surroundings of the orchards, and a more targeted establishment of AES may result in greater benefits to biodiversity and related ecosystem services. Nevertheless, we found a clear positive direct effect of flower cover on pollinator visitation rates of apple flowers (supporting Campbell et al., 2017), which resulted in reduced pollination deficit (measured through seed set) and increased fruit production, suggesting that targeted establishment of flower strips may have positive effects on apple pollination.

When examining the role of natural enemies, we found that higher natural enemy abundance was related to higher fruit production, but this effect was not due to a negative relationship between natural enemy abundance and either aphid abundance or apple pest damage at harvest. This finding suggests that the natural enemies provide some biocontrol that was not captured by our pest sampling. The community of apple pests shows large differences between the different countries, and we therefore had to use relatively coarse measures of damage. It is possible that the natural enemies found in this study mainly regulated earlier pest insects and that this effect is not reflected in our measure of fruit damage. It is also evident that the group of natural enemies is heterogeneous, including spiders, coleopterans, dipterans, neuropterans, heteropterans, earwigs, and harvestmen. Different natural enemies have different diets. Some groups are known to feed on and reduce apple pests (Cross et al., 2015), while the feeding habitats and effects on pest species are less understood for other groups. In addition to pest species, also natural enemies varied in abundance between countries, with a higher abundance of dipterans in Sweden and a higher abundance of heteropterans and earwigs in Germany (A. K. Happe, N. Blüthgen, V. Boreux, J. Bosch, D. García, P. A. Hambäck, A. M. Klein, M. Miñarro, A. Rodrigo, L. Roquer-Beni, U. Samnegård, G. Alins, M. Porcel, R. Martínez Sastre, M. Tassin and K. Mody, unpublished data). It is also evident that our focus on arthropod natural enemies ignore birds, which are known to reduce both caterpillar and aphid damage in apple (García, Miñarro, & Martínez-Sastre, 2018; Mols & Visser, 2002).

Regional differences in management, landscape context, and in the biota on apple trees may affect the effect of organic management versus IPM. For instance, Kehinde, Wehrden, Samways, Klein, and Brittain (2018) found that the bee abundance in vineyards was positively affected by organic management in Italy but not in South Africa, with potential effects on pollination. In our study, we found surprisingly strong regional similarities when comparing organic management and IPM. The SEM coefficients were mostly on the same order with a few exceptions. First, there was a weaker connection between the natural enemy density and fruit damage in Sweden, which may be due to differences in the pest community where winter moth was a dominant pest only in

Sweden. It is possible that the present natural enemies are less able to affect winter moth outbreaks. Second, there was a weaker connection between management and pest damage and aphid abundance in Germany, where aphid control was equally strong in both organic and IPM. Aphid densities during the sampling year may have been low in Germany for other reasons, reducing the effect of management.

In conclusion, our study shows differences in the delivery of ecosystem services between organic and IPM apple orchards, where both natural enemy abundance (measuring biocontrol services) and flower visitation rate (measuring pollination services) were higher in organic orchards. Moreover, pollination services were positively affected by the flower cover surrounding the orchard. Nevertheless, the average IPM orchard reached a higher final apple production even though the variation between orchards was high and the organic orchard with the highest production was producing well above the average IPM orchard. The main reason for the differences in production does not seem to be related to the observed differences in ecosystem services as there was a strong direct (and unexplained) effect of management on apple production. Yet our study also suggests that there is scope for increasing the diversity of beneficial arthropods without reducing production. If differences in species richness between organic and IPM are due mainly to pest control strategies then this pattern would support a continued focus on developing targeted pest control methods that are also environmentally friendly.

ACKNOWLEDGEMENTS

We thank all participating apple growers for allowing us to include their orchard in the project, KOB Bavendorf, FÖKO e.V. and Äppelriket in Kivik, ADV Ecológica de Ponent, and ACTEL, and all field assistants. The research was part of the EcoFruit project funded through the 2013-2014 BiodivERsA/FACCE-JPI joint call (agreement# BiodivERsA-FACCE 2014-74), with the national funders Swedish Research Council Formas (grant# 2014-1784), German Federal Ministry of Education and Research (PT-DLR/BMBF) (grant# 01LC1403), and the Spanish Ministerio de Economía y Competitividad (MINECO) (project# PCIN-2014-145-C02). The research was also funded by Formas grant# 2013-934 (to MT) and project RTA2013-00039-C03-00 funded by Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (to GA). The use of IACS in Sweden was developed within the projects SAPES and MULTAGRI and was adapted to our study by M. Stjernman and P. Olsson.

AUTHORS' CONTRIBUTIONS

A.-M.K., A.-K.H., J.B., K.M., L.R.-B., P.A.H., U.S., and V.B. conceived the ideas for the paper and designed the studies; U.S., G.A., V.B., A.-K.H., M.P., A.R., D.G., M.M., M.T., and L.R.-B. collected the data; U.S. and P.A.H. analysed the data and led the writing of the manuscript. All authors contributed to the development of ideas and drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data for the SEM analysis and the statistical codes are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.3pc3j00> (Samnegård et al., 2019).

ORCID

Daniel García  <http://orcid.org/0000-0002-7334-7836>

Marco Tasin  <http://orcid.org/0000-0001-7379-4954>

Peter A. Hambäck  <http://orcid.org/0000-0001-6362-6199>

REFERENCES

- Albert, L., Franck, P., Gilles, Y., & Plantegenest, M. (2017). Impact of agro-ecological infrastructures on the dynamics of *Dysaphis plantaginea* (Hemiptera: Aphididae) and its natural enemies in apple orchards in Northwestern France. *Environmental Entomology*, 46, 528–537. <https://doi.org/10.1093/ee/nvx054>
- Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29, 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Berry, P. M., Sylvester-Bradley, R., Philipps, L., Hatch, D. J., Cuttle, S. P., Rayns, F. W., & Gosling, P. (2002). Is the productivity of organic farms restricted by the supply of available nitrogen? *Soil Use and Management*, 18, 248–255. <https://doi.org/10.1079/SUM2002129>
- Blommers, L. H. (1994). Integrated pest management in European apple orchards. *Annual Review of Entomology*, 39, 213–241. <https://doi.org/10.1146/annurev.en.39.010194.001241>
- Breeze, T. D., Bailey, A. P., Balcombe, K. G., & Potts, S. G. (2011). Pollination services in the UK: How important are honeybees? *Agriculture Ecosystems & Environment*, 142, 137–143. <https://doi.org/10.1016/j.agee.2011.03.020>
- Campbell, A. J., Wilby, A., Sutton, P., & Wackers, F. L. (2017). Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture Ecosystems & Environment*, 239, 20–29. <https://doi.org/10.1016/j.agee.2017.01.005>
- Carreras, J., & Diego, F. (2009). *Catalan habitats cartography*, 1:50,000. Barcelona, Spain: Departament de Medi Ambient i Habitatge, Generalitat de Catalunya.
- Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T. C., Anshary, A., & Tschardt, T. (2011). Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 8311–8316. <https://doi.org/10.1073/pnas.1016799108>
- Cross, J., Fountain, M., Marko, V., & Nagy, C. (2015). Arthropod ecosystem services in apple orchards and their economic benefits. *Ecological Entomology*, 40, 82–96. <https://doi.org/10.1111/een.12234>
- de Ponti, T., Rijk, B., & van Ittersum, M. K. (2012). The crop yield gap between organic and conventional agriculture. *Agricultural Systems*, 108, 1–9. <https://doi.org/10.1016/j.agsy.2011.12.004>
- Dib, H., Sauphanor, B., & Capowiez, Y. (2016). Effect of management strategies on arthropod communities in the colonies of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) in south-eastern France. *Agriculture Ecosystems & Environment*, 216, 203–206. <https://doi.org/10.1016/j.agee.2015.10.003>
- FAO (2018). Food and Agriculture Organization of the United Nations, Retrieved from <http://www.fao.org/statistics> (Accessed 24 February 2018).
- Fountain, M. T., & Harris, A. L. (2015). Non-target consequences of insecticides used in apple and pear orchards for *Forficula auricularia* L. (Dermaptera: Forficulidae). *Biological Control*, 91, 27–33. <https://doi.org/10.1016/j.biocontrol.2015.07.007>
- Gabriel, D., Sait, S. M., Kunin, W. E., & Benton, T. G. (2013). Food production vs. biodiversity: Comparing organic and conventional agriculture. *Journal of Applied Ecology*, 50, 355–364. <https://doi.org/10.1111/1365-2664.12035>
- García, D., Miñarro, M., & Martínez-Sastre, R. (2018). Birds as suppliers of pest control in cider apple orchards: Avian biodiversity drivers and insectivory effect. *Agriculture Ecosystems & Environment*, 254, 233–243. <https://doi.org/10.1016/j.agee.2017.11.034>
- Garratt, M. P. D., Breeze, T. D., Boreux, V., Fountain, M. T., Mc Kerchar, M., Webber, S. M., ... Potts, S. G. (2016). Apple pollination: Demand depends on variety and supply depends on pollinator identity. *PLoS ONE*, 11, e0153889. <https://doi.org/10.1371/journal.pone.0153889>
- Granatstein, D., & Sánchez, E. (2009). Research knowledge and needs for orchard floor management in organic tree fruit systems. *International Journal of Fruit Science*, 9, 257–281. <https://doi.org/10.1080/15538360903245212>
- Gurr, G. M., Wratten, S. D., & Luna, J. M. (2003). Multi-function agricultural biodiversity: Pest management and other benefits. *Basic and Applied Ecology*, 4, 107–116. <https://doi.org/10.1078/1439-1791-00122>
- Hohenstein, S., & Kliegl, R. (2015). Remove partial effects, R package version 1.0.6.9000.
- Joshi, N. K., Otieno, M., Rajotte, E. G., Fleischer, S. J., & Biddinger, D. J. (2016). Proximity to woodland and landscape structure drives pollinator visitation in apple orchard ecosystem. *Frontiers in ecology and evolution*, 4, 38.
- Kehinde, T., Wehrden, H., Samways, M., Klein, A. M., & Brittain, C. (2018). Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *Journal of Insect Conservation*, 22, 61–67. <https://doi.org/10.1007/s10841-017-0038-4>
- Kendall, D. A. (1973). Viability and compatibility of pollen on insects visiting apple blossom. *Journal of Applied Ecology*, 10, 847–853. <https://doi.org/10.2307/2401873>
- Klein, A. M., Fornoff, F., Mupepele, A. C., & Boreux, V. (2018). Relevance of wild and managed bees for human well-being. *Current Opinion in Insect Science*, 26, 82–88. <https://doi.org/10.1016/j.cois.2018.02.011>
- Klein, A. M., Hendrix, S. D., Clough, Y., Scofield, A., & Kremen, C. (2015). Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biology*, 17, 201–208. <https://doi.org/10.1111/plb.12180>
- Kühn, I., Durka, W., & Klotz, S. (2004). BioFlor – A new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, 10, 363–365.
- Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, 18, 1–12. <https://doi.org/10.1016/j.baae.2016.07.005>
- Lefcheck, J. S. (2016). Piecewise structural equation modelling. R package version 1.2.1.
- Lefebvre, M., Franck, P., Olivares, J., Ricard, J. M., Mandrin, J. F., & Lavigne, C. (2017). Spider predation on rosy apple aphid in conventional, organic and insecticide-free orchards and its impact on aphid populations. *Biological Control*, 104, 57–65. <https://doi.org/10.1016/j.biocontrol.2016.10.009>
- LGL. (2016). *ATKIS Digitales Landschaftsmodell, Baden-Württemberg, Basis-DLM Version 6.0*. Landesamt für Geoinformation und Landentwicklung.
- Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batary, P., Berendse, F., Bommarco, R., ... Crowder, D. W. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within

- fields and across agricultural landscapes. *Global Change Biology*, 23, 4946–4957. <https://doi.org/10.1111/gcb.13714>
- Malavolta, C., & Cross, J.V. (2009). Guidelines for integrated production of pome fruits in Europe, IOBC Technical Guideline III (Vol. 47, 4th ed., pp. 1–12). IOPC/wprs Bulletin.
- Mallinger, R. E., & Gratton, C. (2015). Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology*, 52, 323–330. <https://doi.org/10.1111/1365-2664.12377>
- Marini, L., Quaranta, M., Fontana, P., Biesmeijer, J. C., & Bommarco, R. (2012). Landscape context and elevation affect pollinator communities in intensive apple orchards. *Basic and Applied Ecology*, 13, 681–689. <https://doi.org/10.1016/j.baae.2012.09.003>
- Miñarro, M., & Prida, E. (2013). Hedgerows surrounding organic apple orchards in north-west Spain: Potential to conserve beneficial insects. *Agricultural and Forest Entomology*, 15, 382–390. <https://doi.org/10.1111/afe.12025>
- Mols, C. M. M., & Visser, M. E. (2002). Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology*, 39, 888–899. <https://doi.org/10.1046/j.1365-2664.2002.00761.x>
- Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E., & Danforth, B. N. (2015). Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B-Biological Sciences*, 282, 20150299. <https://doi.org/10.1098/rspb.2015.0299>
- Pisa, L. W., Amaral-Rogers, V., Belzunces, L. P., Bonmatin, J. M., Downs, C. A., Goulson, D., & Wiemers, M. (2015). Effects of neonicotinoids and fipronil on non-target invertebrates. *Environmental Science and Pollution Research*, 22, 68–102. <https://doi.org/10.1007/s11356-014-3471-x>
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Power, A. G. (2010). Ecosystem services and agriculture: Tradeoffs and synergies. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 365, 2959–2971. <https://doi.org/10.1098/rstb.2010.0143>
- Primdahl, J., Peco, B., Schramek, J., Andersen, E., & Onate, J. J. (2003). Environmental effects of agri-environmental schemes in Western Europe. *Journal of Environmental Management*, 67, 129–138. [https://doi.org/10.1016/S0301-4797\(02\)00192-5](https://doi.org/10.1016/S0301-4797(02)00192-5)
- Ramirez, F., & Davenport, T. L. (2013). Apple pollination: A review. *Scientia Horticulturae*, 162, 188–203. <https://doi.org/10.1016/j.scienta.2013.08.007>
- Reganold, J. P., Glover, J. D., Andrews, P. K., & Hinman, H. R. (2001). Sustainability of three apple production systems. *Nature*, 410, 926–930. <https://doi.org/10.1038/35073574>
- Rundlöf, M., Nilsson, H., & Smith, H. G. (2008). Interacting effects of farming practice and landscape context on bumblebees. *Biological Conservation*, 141, 417–426. <https://doi.org/10.1016/j.biocon.2007.10.011>
- Rusch, A., Birkhofer, K., Bommarco, R., Smith, H. G., & Ekblom, B. (2014). Management intensity at field and landscape levels affects the structure of generalist predator communities. *Oecologia*, 175, 971–983. <https://doi.org/10.1007/s00442-014-2949-z>
- Samnegård, U., Alins, G., Boreux, V., Bosch, J., García, D., Happe, A.-K., ... Hambäck, P. A. (2019). Data from: Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect effects of organic production. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.3pc3j00>
- Saunders, M. E., & Luck, G. W. (2018). Interaction effects between local flower richness and distance to natural woodland on pest and beneficial insects in apple orchards. *Agricultural and Forest Entomology*, 20, 279–287. <https://doi.org/10.1111/afe.12258>
- Saunders, M. E., Peisley, R. K., Rader, R., & Luck, G. W. (2016). Pollinators, pests, and predators: Recognizing ecological trade-offs in agroecosystems. *Ambio*, 45, 4–14. <https://doi.org/10.1007/s13280-015-0696-y>
- Seufert, V., Ramankutty, N., & Foley, J. A. (2012). Comparing the yields of organic and conventional agriculture. *Nature*, 485, 229–U113. <https://doi.org/10.1038/nature11069>
- Shackelford, G., Steward, P. R., Benton, T. G., Kunin, W. E., Potts, S. G., Biesmeijer, J. C., & Sait, S. M. (2013). Comparison of pollinators and natural enemies: A meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, 88, 1002–1021. <https://doi.org/10.1111/brv.12040>
- Simon, S., Bouvier, J. C., Debras, J. F., & Sauphanor, B. (2010). Biodiversity and pest management in orchard systems. A review. *Agronomy for Sustainable Development*, 30, 139–152. <https://doi.org/10.1051/agro/2009013>
- SIOSE. (2015). *Spanish Habitats Cartography, 1:25,000. Equipo Técnico Nacional SIOSE, Spanish Land Use and Land Cover Information System*. Ministerio de Fomento. Centro Nacional de Información Geográfica, Madrid.
- Stanley, D. A., Garratt, M. P. D., Wickens, J. B., Wickens, V. J., Potts, S. G., & Raine, N. E. (2015). Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature*, 528, 548–552. <https://doi.org/10.1038/nature16167>
- Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., ... Zhang, W. (2016). When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*, 204, 449–458. <https://doi.org/10.1016/j.biocon.2016.10.001>
- Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17, 910–921. <https://doi.org/10.1890/06-0269>
- Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E., & Desneux, N. (2012). Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture Ecosystems & Environment*, 159, 112–122. <https://doi.org/10.1016/j.agee.2012.06.020>

How to cite this article: Samnegård U, Alins G, Boreux V, et al. Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect effects of organic production. *J Appl Ecol*. 2018;00:1–10. <https://doi.org/10.1111/1365-2664.13292>